Aspects of the ecology and behaviour of ringed and grey plovers charadrius hiaticula and pluvialis squatarola

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Aspects of the Ecology and Behaviour of Ringed and Grey Plovers *Charadrius hiaticula* and *Pluvialis squatarola*

by

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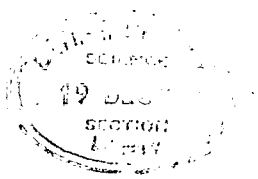

To my parents,
Michal Stefan
and
Winifred Maria
Piefikowski

ASPECTS OF THE ECOLOGY AND BEHAVIOUR OF RINGED AND GREY PLOVERS *CHARADRIUS HIATICULA* AND *PLUVIALIS SQUATAROLA*

Abstract

Both plovers were studied at Lindisfarne, Northumberland, during three non-breeding seasons; and the Ringed Plover while breeding at Lindisfarne and in NE Greenland.

In winter both species fed principally on intertidal polychaetes, but prey differed in different sites. Food requirements in winter could not be met during daylight. Prey capture rate at night was lower than by day. Plovers carry large fat reserves in winter probably to buffer the effects of cold, windy weather, which reduces their feeding rates more than those of sandpipers.

Plovers search for prey apparently by visual means (without the tactile element used by other waders). At the sand surface intertidal invertebrates increased their activity (which enabled plovers to detect them) with increasing temperature; also in some cases with foot-vibration by Ringed Plovers. With an increase in prey availability, the birds increased their capture rate first and then their selectivity of prey sizes and species. A simple model is developed to describe the foraging behaviour and its modifications in relation to prey availability and distribution. The presence of other shorebirds also affected prey capture rate. Nocturnal foraging is discussed in relation to visual foraging and invertebrate activity. An attempt is made to predict the minimum densities of prey required for energy balance in various conditions and to compare visual and tactile foraging strategies of plovers and sandpipers.

Growth rates of Ringed Plover chicks were similar in all areas and diurnal rhythm in activity more marked in the Arctic. The development of foraging from hatching to first winter is described in comparison to that of adults and survival rates for various age-groups assessed. Food supply does not appear to limit growth or chick survival but feeding ability may become important in autumn.

Territory establishment, distribution and size, the timing of laying, clutch size, incubation schedules and nesting success are compared for different areas. Predation was the main cause of the very variable nesting success in different areas and appears to be the major determinant of timing of nesting and the limit of the breeding range in temperate areas. The influence of human disturbance and possible conservation measures are discussed.

Contents

Contents (cont.)

Acknowledgements

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The geographical comparisons concerning the breeding season benefited greatly by unpublished information supplied by N.K. Atkinson, Miss C.M. Lessells, J. Sheldon, J.R. Wilson and the National Trust Farnes Island wardens 1975. The British Trust for Ornithology Populations and Surveys Committee kindly allowed me to borrow and investigate their Nest Record Cards for Ringed Plovers. I am grateful to those people who reported sightings of colour-ringed Ringed Plovers and to Dr A. Siefke of Vogelwarte Hiddensee for information on his colour-marking scheme for this species.

Dr P. Garwood, University of Newcastle, kindly confirmed my identifications of polychaetes. Unpublished information on various matters was readily supplied by several colleagues at the Zoology Department, Durham University, particularly N.C. Davidson, P.J. Dugan, A.V. Millard, P.C. Smith and D.J. Townshend.

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I have considerable doubts that this thesis would ever have been completed, at least in anything like its present form, without the help of my wife, Ann. Not only did she allow her kitchen to be turned into a laboratory, lounge into office and bedroom into library, but also frequently collaborated in this, by helping sample and count invertebrates, coding much of the behavioural information and typing this thesis. Our daughter, Clare, found a use for large quantities of sand no longer required by their former occupants.

General Introduction

The coastal wetlands of Western Europe provide habitats in the long non-breeding season for large numbers of wading birds of several species which breed in arctic regions from NE Canada to Siberia. Among these are the Grey Plover *Pluvialis squatarola*, which breeds in Siberia, and the smaller Ringed Plover *Charadrius hiaticula* whose breeding range extends from the high Arctic of Greenland and Siberia as far south as Britain. Individuals of both species may spend nine or ten months of every year in the "wintering" areas.

In recent years several studies of the winter ecology and behaviour of wading birds have been undertaken in W. Europe, partly because the shorebird-predator/invertebrate-prey system is an interesting one for study and these birds of open habitats are reasonably easy to observe, but also because industrial activities and large-scale reclamations are threatening many of the intertidal habitats of these birds. Thus information on their ecological requirements is urgently needed.

Previous detailed studies have concerned chiefly the sandpiper family Scolopacidae and the Oystercatcher *Haematopus ostralegus* both of which include a strong element of tactile searching with their bills while foraging. The plovers (family Charadriidae) which form the other main component of the shorebird community forage by very different techniques, apparently dependent on visual searching. The initial aim of this study which took place from October 1973 to September 1976 was to obtain detailed information on their feeding ecology and foraging behaviour to allow comparison with those of the other shore waders.

The Ringed Plover also provided an opportunity for studying other questions as it is a common breeding bird in summer at Lindisfarne National Nature Reserve, Northumberland, the main area used for the winter observations. It was thus possible to study the feeding ecology of the same species, and possibly some of the same individuals throughout the whole year, and to examine its breeding biology and aspects of its population dynamics. In summer 1974, I was able to extend the breeding study by spending two months in Greenland collecting data from one of the northerly breeding populations for comparison with that from the southern end of the range. Ringed Plovers have been the subject of

several previous breeding season studies, notably that of Laven (1940), but these have tended to be concerned mainly with descriptions of territory, behaviour, density and hatching success; and have been mainly confined to Europe. In the present study, I was concerned to include other aspects of the birds' biology, such as feeding in the breeding season, and to compare this and the breeding production in high arctic and temperate regions.

Perhaps the aspect of wader studies most neglected so far is that of the development of the chicks from hatching until after fledging. Because at this time most wader young are extremely difficult to observe in the tundras or other vegetation of their breeding areas, very little is known of their feeding, growth and survival rates. Although Ringed Plover young are also highly cryptic and hide in any vegetation available, this species uses fairly unvegetated breeding areas so is slightly less difficult to study. Much of my work during the breeding season at both Lindisfarne and NE Greenland was concentrated on the young.

This thesis is presented as four papers (which, it is hoped, may be suitable for publication without major changes in format) and five appendices. The first two papers are concerned with the winter feeding ecology and behaviour of the two plover species, the third with the development of foraging behaviours, growth and survival to reproductive age of the young Ringed Plovers, and the fourth with other aspects of the breeding biology and population dynamics of Ringed Plovers. The appendices provide further supporting information on various aspects covered in the main papers.

Paper 1. The feeding ecology of Grey and Ringed Plovers in the non-breeding season

INTRODUCTION

The recent increase in pressure on intertidal habitats by reclamation for industrial and other purposes has increased the need for studies of the habitat requirements of the various species of shore-birds. Detailed investigations have been made on a number of waders but all have been concerned primarily with the sandpiper family Scolopacidae or the Oystercatcher *Haematopus ostralegus* (e.g. Bengtson & Svensson 1968, Dare & Mercer 1973, Davidson 1967, Drinnan 1958, Ehlert 1964, Feare 1966, Fuchs 1975, Goss-Custard 1969, 1970a,b, 1977b, Heppleston 1971, Hulscher 1974, 1976, Norton-Griffiths 1967, Prater 1972, Recher 1966, Smith & Evans 1973, Spitz 1964, Thomas & Dartnall 1971, Vielliard 1973). The present study is concerned with the other main family of shore-birds, the plovers Charadriidae which forage by an apparently visual technique without the element of tactile searching normally used by the other waders (e.g. Burton 1974).

This paper reports first the diet of Grey Plovers *Pluvialis squatarola* and Ringed Plovers *Charadrius hiaticula* at Lindisfarne, Northumberland, in the winters of 1973-4, 74-75 and 75-76 and compares this with diets reported elsewhere, second describes attempts to estimate the impact of these predators on some of their prey species at Lindisfarne, and third considers the amount of food eaten by the plovers in daylight hours and the extent of nocturnal feeding, and discusses the question of energy balance.

STUDY AREA

Lindisfarne National Nature Reserve (Fig. 1) in north Northumberland comprises about 3240 hectares (12½ square miles), mainly of tidal mud and sandflats, saltmarsh and dunes.

My research was concentrated mainly on the eastern and northern parts of Holy Island Sands (abbreviated henceforth to HIS). This predominantly sandy area of about 750 hectares, characterised by casts

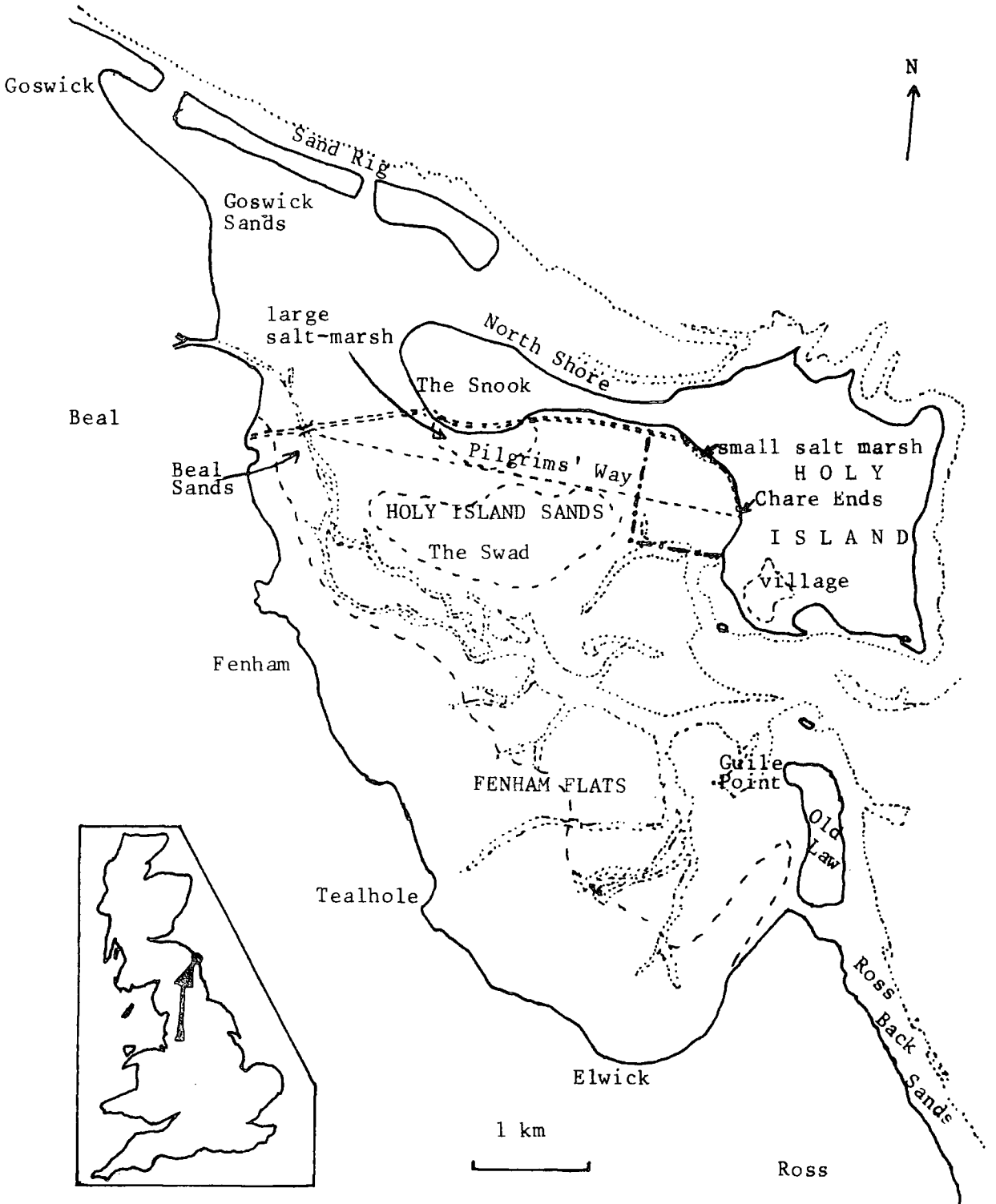


Figure 1. The intertidal sand- and mud-flats at Lindisfarne, Northumberland, with inset showing location.

..... low water of normal spring tides
——— high water of normal spring tides
- - - - limits of mud occurring on the Swad and upper Fenham Flats; line of Pilgrims' Way
===== Causeway
—·—·— limits of Figure 4 (main study area)

formed by lugworms *Arenicola marina*, forms a wide strip between Holy Island and the muddier part of HIS, the Swad, consisting of about 1100 hectares with extensive eel-grass *Zostera* spp with some areas of cord-grass *Spartina* spp.

The sandy region was the main winter feeding area of the Ringed Plovers and one of the main areas of Grey Plovers, the latter also using, particularly at low water, other parts of the reserve, especially the sandy banks south of the main study area and west of Holy Island village and the muddy area of Fenham Flats on the mainland side of the reserve, where only a few observations were made.

Some observations were also made on the north shore of Holy Island Snook (henceforth termed the North Shore) where Ringed Plovers in particular congregated on some occasions in the winter and where a flock formed before pre-breeding territories were taken up, at first temporarily, from February onwards.

The general movements of the birds about the area in relation to the tide are summarized in Figure 2 which also gives the distribution of some important prey (see below) as indicated by a survey on a ½ km grid in May and June 1973 by W.F. Miller and A. Turk (unpublished). The patterns of usage of areas appeared similar on spring and neap tides.

METHODS

Diet and feeding rates

Goss-Custard (1973) reviewed the methods available and their limitations for the determination of diet of shore-birds. At Lindisfarne, neither Ringed nor Grey Plover have been observed to regurgitate pellets of indigestible material and no identifiable prey remains were found in a number of faecal pellets of both species examined.

The gut contents of two Grey Plovers were examined. One was shot on 20 March 1973 as it flew from HIS to roost. The oesophagus was empty and there were no identifiable prey in the intestine. The

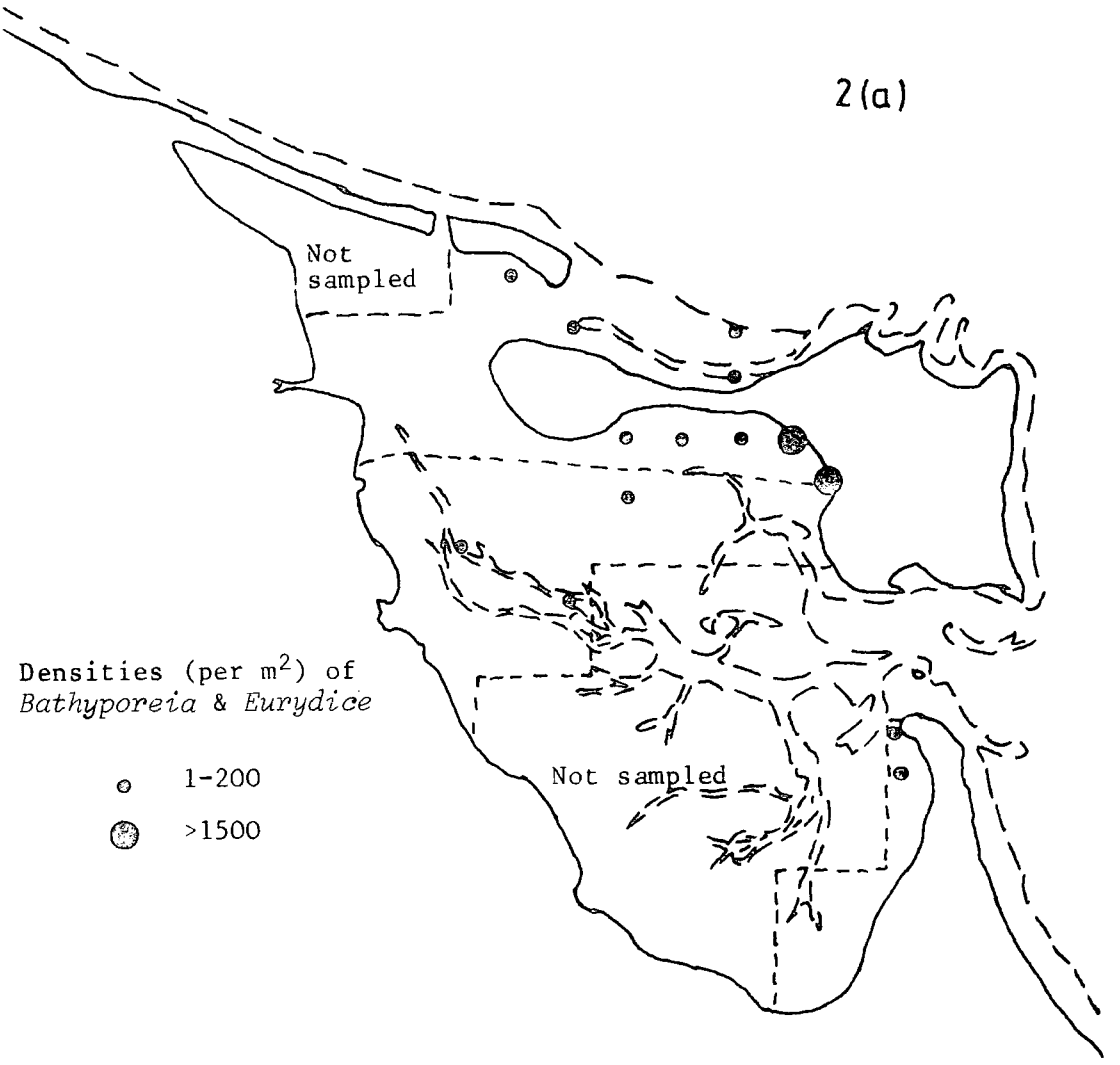


Figure 2. General distributions of Ringed and Grey Plovers and some of their main prey at Lindisfarne NNR.

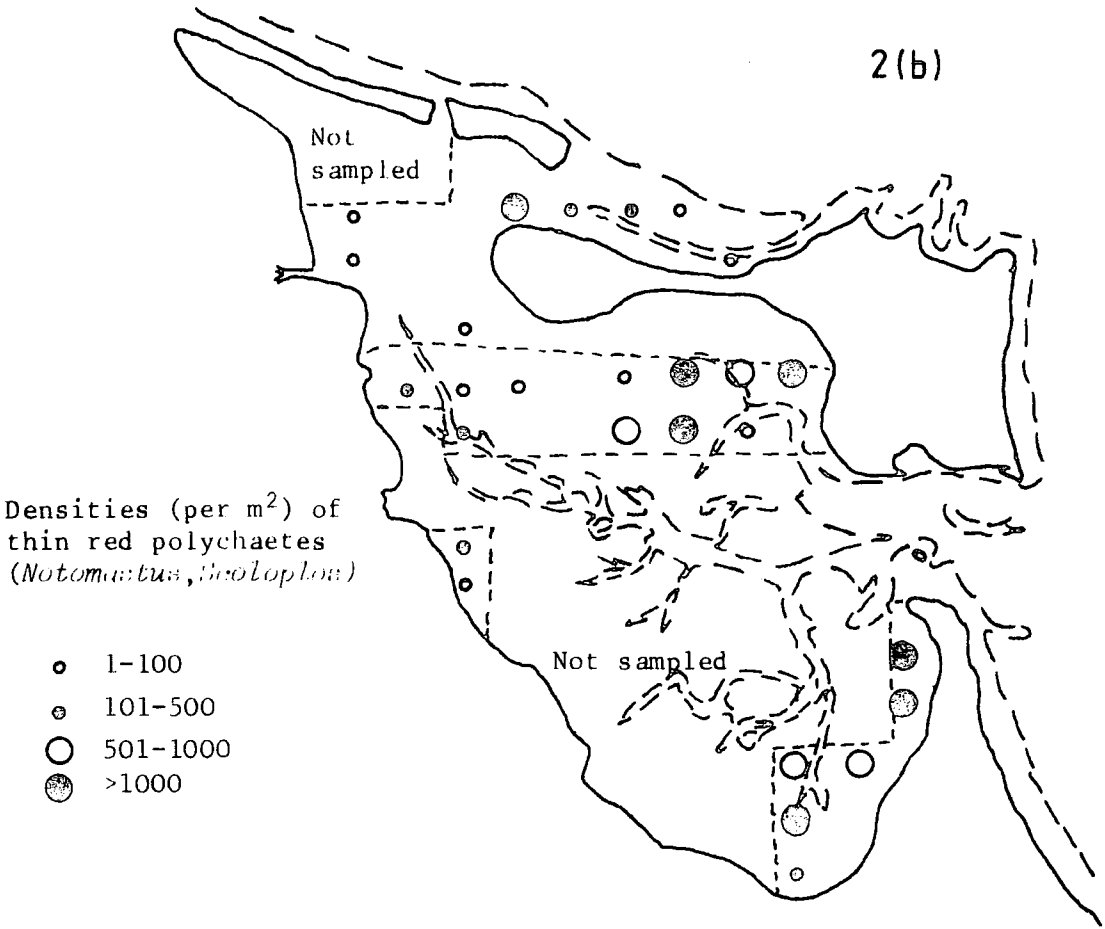
(a) *Bathyporeia & Eurydice*

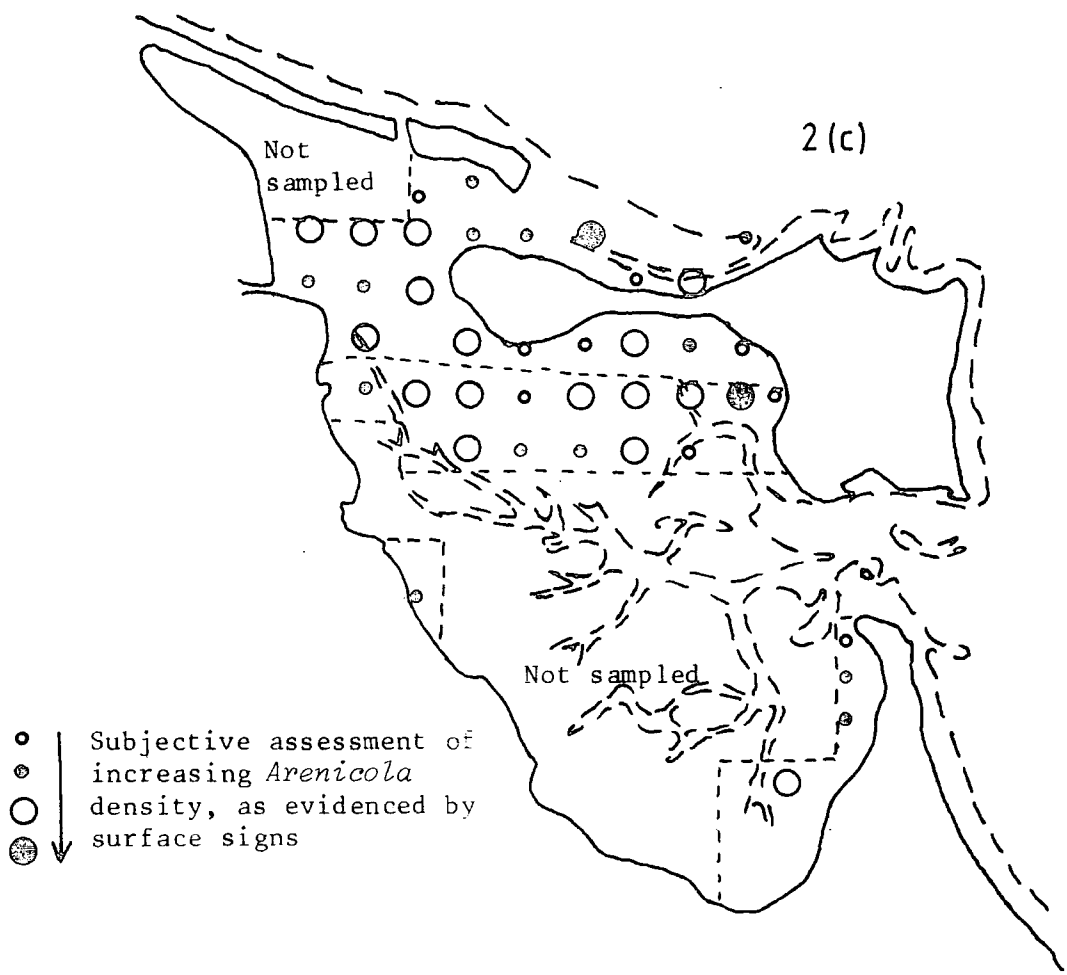
(b) Thin red polychaetes (*Notomastus & Scoloplos*)

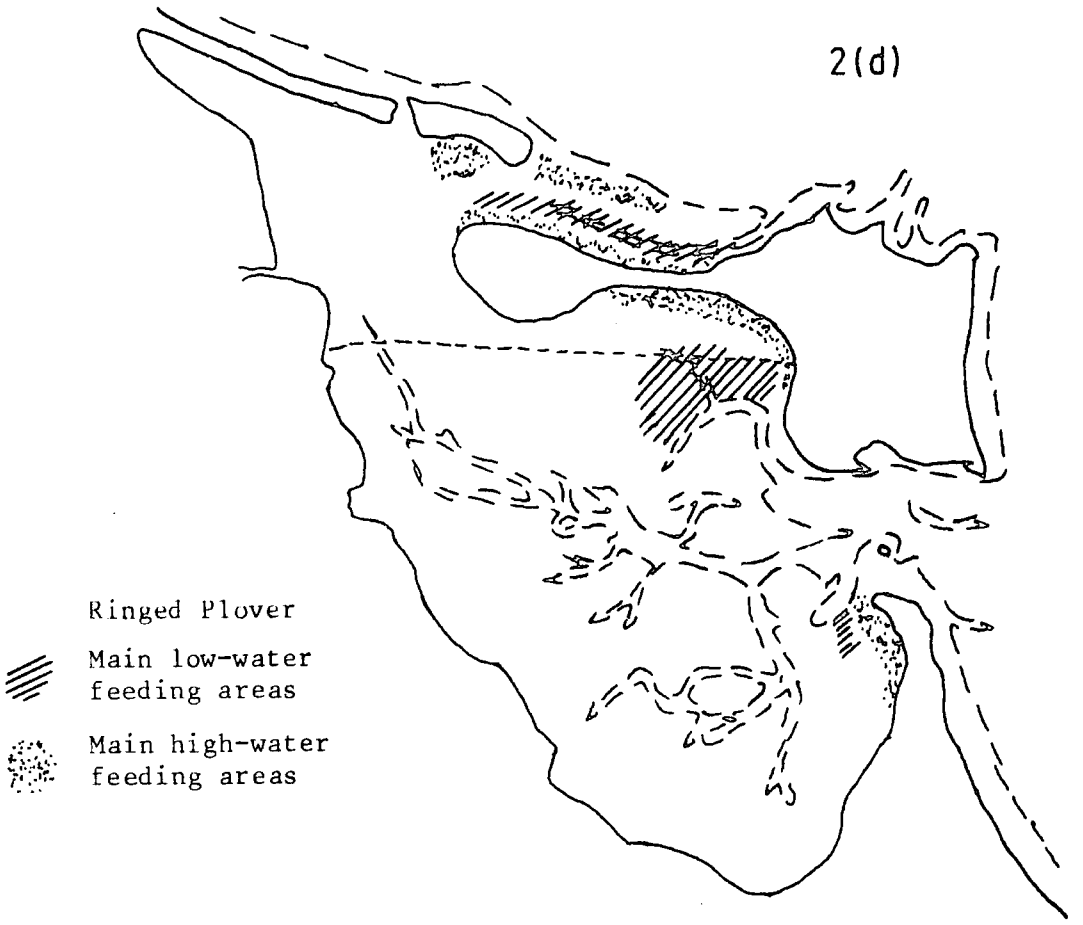
(c) *Arenicola*

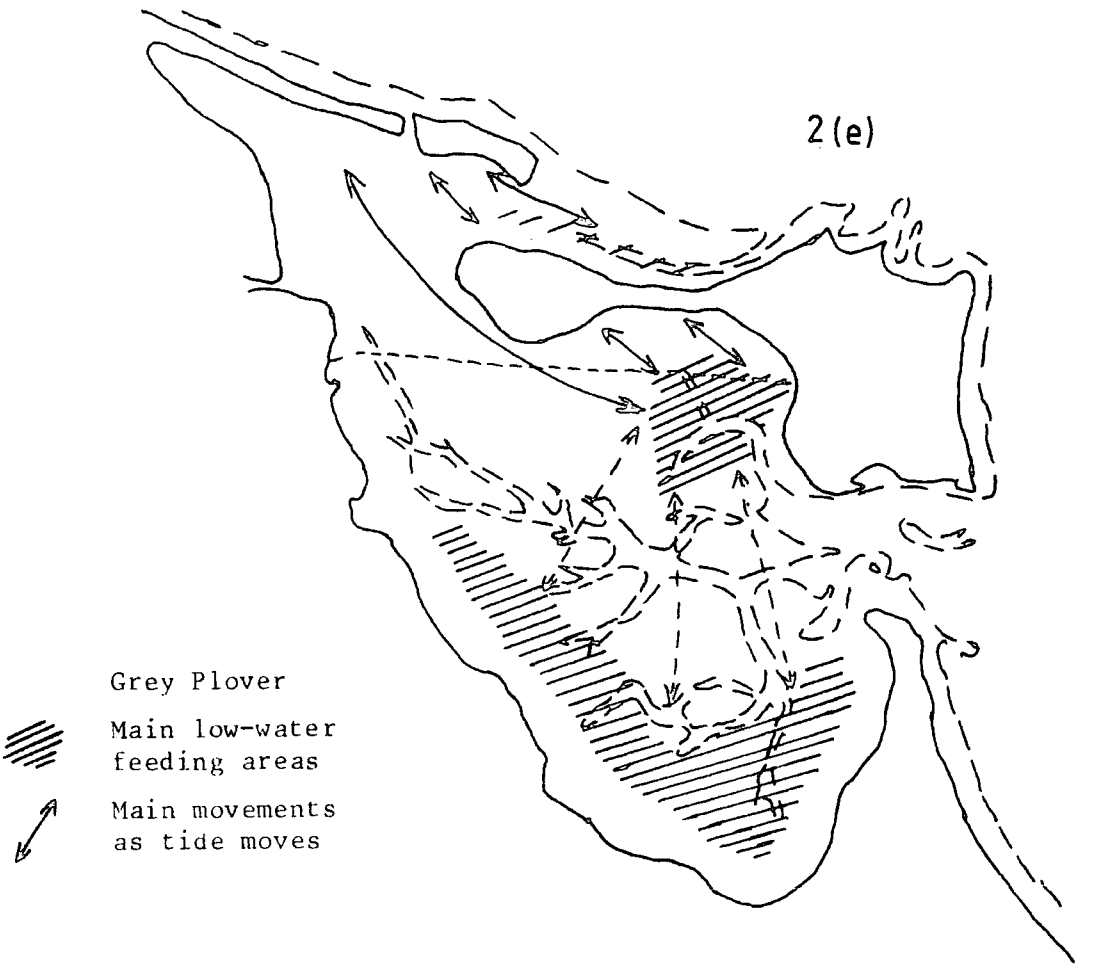
(d) Ringed Plover

(e) Grey Plover


2(b)
Not sampled
Not sampled
Densities (per m²) of thin red polychaetes (Notomastus, Sabellaria)
1-100
101-500
501-1000
>1000


2(c)
Not sampled
Not sampled
Subjective assessment of increasing Arenicola density, as evidenced by surface signs


2(d)
Ringed Plover
Main low-water feeding areas
Main high-water feeding areas


2(e)
Grey Plover
Main low-water feeding areas
Main movements as tide moves

gizzard held six intact shells of the gastropod *Gibbula umbilicalis*, six broken shells of the gastropod *Littorina* sp., 1 fragment of shell of the bivalve *Cerastoderma* sp., 1 fragment of crab leg and several smaller unidentifiable shell fragments and possibly a little vegetable matter. No soft-bodied prey were recognizable. The other was shot on 22 October 1974 while feeding on HIS. Immediately before collection the bird had taken a series of thin red worms, *Notomastus latericeus* possibly with *Scoloplos armiger* (see below). The gut was removed and preserved within about three minutes of the time the bird stopped feeding. Again no prey were found in the oesophagus and no remains in the intestine were identifiable. In the gizzard, only four pieces of *Notomastus* were identifiable, probably parts of two worms. Also present were one short piece (about 1 cm long) of *Arenicola marina*, carapace, pincers and legs of one crab *Carcinus maenas*, 1 shell and numerous fragments of the bivalve *Macoma balthica* and a few small fragments of vegetable matter.

These two examples illustrate some of the problems of analysis of gut contents as a basis of prey identification. *Gibbula* is a rocky shore mollusc and has not been identified in extensive sampling on HIS. Presumably the bird had encountered a small concentration or had taken them before moving to HIS. The absence of soft-bodied prey in the gut, despite these being the most frequent items seen to be taken on HIS (see below) is notable. The bird shot while feeding did contain a fragment of *Arenicola* and remains of *Notomastus* (but in very small numbers), whereas these had been the only prey seen to be taken in that area prior to collection. *Carcinus* and *Macoma*, two infrequent prey, were however, well preserved.

Smith (1975) has demonstrated that soft-bodied worms as large as *Arenicola* can be digested without trace by Bar-tailed Godwits *Limosa lapponica* within little over one minute but that hard fragments, such as mandibles of *Nereis*, may be retained for at least six months. The lack of identifiable prey fragments in the intestine and droppings of plovers at Lindisfarne and the absence of regurgitated pellets is thus not surprising as field observations of feeding birds and sampling of substrate (see below) indicate that the diet of both species at Lindisfarne comprises largely soft-bodied worms.

Goss-Custard (1973, 1977c) showed that valid and reliable information on prey composition and feeding rates can be obtained by field observations of feeding birds, and this approach was adopted also in my study. Observations were made initially from a 'hide' consisting of bales of straw anchored to the mud surface, a method used successfully in the study of Bar-tailed Godwits at Lindisfarne by Smith (1975). However, this method proved unsuitable for the more mobile flocks of plovers which did not restrict their feeding to the vicinity of the tide edge. Most observations were therefore made from a car parked on the sand-flats and moved when necessary.

Observations were made with a 15 x to 60 x telescope, of individual feeding birds, normally over periods of one to two minutes. The numbers and, where visible, types of prey taken were recorded, as were various other behavioural details (see Paper 2), weather conditions, proximity of other birds, etc. At intervals of about 15 minutes, the numbers of each species feeding or engaged in other activities were noted.

Some prey, such as lugworms *Arenicola*, crabs (mainly *Carcinus*), and ragworms (principally *Nereis diversicolor*, as indicated by substrate sampling) were easily identifiable. *Arenicola* was distinctive because of its size and shape and its fairly inert appearance while hanging from the bird's bill. The length of worm as it hung from the bill was estimated in relation to the height of the bill from the ground (approximately 80 mm in Ringed Plovers and 120 mm in Grey Plovers - measured from still and ciné photography, mounted specimens and live birds caught). Short pieces of the tails of *Arenicola* were sometimes taken and the lengths of these were estimated in relation to bill length (about 15 mm in Ringed Plover and 30 mm in Grey Plover). Ragworms (principally *Nereis diversicolor*) were recognisable because of their 'ragged' appearance and their tendency to writhe rhythmically while suspended from the bill. Crabs had a distinctive appearance and the birds dealt with them in a characteristic manner: holding by each leg in turn and shaking to detach this from the body before swallowing, and usually finishing by swallowing the main body. Also easily recognisable in the field were pieces of green algae taken by the birds; it was not possible to see whether any small animals were attached to

these when swallowed, although the prosobranch *Hydrobia ulvae* is known to favour algal mats.

Other prey items - the majority - were smaller and, although it was possible to identify these on many occasions, there were many pecks which could only be allocated to either "successful peck, prey unknown" or " peck, outcome unknown". The most important of these smaller prey were clearly thin worms, mainly red-bodied. When seen, the lengths of these worms were estimated in relation to bill-height while the worm was stretched as the plover pulled it from its burrow.

Identification of thin worms as prey was aided by the distinctive behaviour of the plover while taking the prey. The bird darted to peck at the ground, then pulled the worm from the ground, initially holding the bill pointing almost vertically downwards. The bill, head and body pivoted upwards slowly as the worm emerged and on some occasions with long worms the bird quickly transferred its grip to lower parts of the worms' bodies. Finally, the bird's head was flicked rapidly as the worm came free and was swallowed. Plovers feeding in this manner often showed fine dark lines across their breasts where the muddy worms had lashed as they came free from their burrows.

To test the validity of 'thin worm' identification and to investigate the nature of other pecks, colour ciné film was taken of birds feeding in the natural situation. The processed film was then run at normal speed and data recorded as in the field. The film was later analysed frame by frame to identify prey taken. Many months elapsed between making and watching the film and between watching and frame-by-frame analysis, during which time many other birds were watched in the field and on film, so that there is little likelihood of memory retention of previous assessments. The film analysis gave a conservative assessment of the identification ability of the observer as viewing conditions were less good by film than by direct observation. This resulted from limitations of equipment and operator, poor light for filming and low power of telephoto lens compared with telescope. Comparison of prey observed with that recorded by frame-by-frame analysis is given for the two plovers in Table 1.

TABLE 1. COMPARISON OF PREY RECORDED FROM FILM RUN AT NORMAL SPEED WITH THAT REVEALED BY FRAME-BY-FRAME ANALYSIS.

GREY PLOVER

		normal speed			
		peck	peck, small prey	peck, thin worm	Total
		no. (%)	no. (%)	no. (%)	no. (%)
frame-by-frame	p.	1 (14.3)	2[2] (10.0)	1[1] (5.9)	4 (9.1)
	ps.	1 (14.3)	4 (20.0)	0 (0)	5 (11.4)
	pw.	5 (71.4)	14 (70.0)	16 (94.1)	35 (79.5)
	Total	7	20	17	44

RINGED PLOVER

		normal speed			
		peck	peck, small prey	peck, thin worm	Total
		no. (%)	no. (%)	no. (%)	no. (%)
frame-by-frame	p.	2 (22.2)	12[2] (14.3)	1[1] (3.2)	15 (12.1)
	ps.	2 (22.2)	34 (40.5)	7[1] (22.6)	43 (34.7)
	pw.	5 (55.6)	38 (45.2)	23 (74.2)	66 (53.2)
	Total	9	84	31	124

Notes [1] Re-showing of film clearly indicated these to be worms because of characteristic bird feeding movements although the worms themselves could not be seen.

[2] During re-showing bird movement suggested that small prey were taken but these were not visible.

It was not always possible to assess worm length from the film record and most were fairly small. However, those that were measurable supported the estimate made when the film had been run at normal speed.

Table 1 demonstrates that the identification of thin worms by the method used in the field was valid and that the recording of items as "peck" or "successful peck" was conservative in that most of these were captures of thin worms. At most, 9% of Grey Plover pecks and 12% of Ringed Plover pecks were unsuccessful, more likely figures being 2% for each species. This is consistent with a finding that 99.4% of 943 pecks of Grey Plovers at Teesmouth, County Cleveland, resulted in prey being taken (Pienkowski 1973). In Connecticut Baker (1974) estimated that Black-bellied Plovers (the same species) on autumn and spring migration were successful in only 48% and 40% of pecks respectively. It is difficult to see the reason for this difference or determine whether it is real or due to differences in interpretation. Possibly, without a check from ciné-film, Baker allocated the equivalent of my 'pecks with unknown outcome' to 'unsuccessful' and was more conservative in allocating prey types. In any event, because of the very small relative calorific value of small prey (see below), the difference between unsuccessful peck and small prey (even in considerable numbers) in terms of contribution to energy intake is small. Further consideration of validity and reliability of my observations of feeding behaviour are made in Paper 2.

Details of prey and feeding rates were normally recorded as prey were taken by talking into a continually running tape recorder. The information was later filed on punch cards and sorted into number and capture rate of each type of prey taken, and various behavioural categories by a specially written computer program 'PLOVPROG' (see Appendix 3 for a listing of 'PLOVPROG' and Paper 2 for more details of procedure). The sorted material was stored on magnetic tape. Analyses usually employed the statistical procedures available in the package SPSS (Nie et al 1975). Other statistical procedures follow Bailey (1959) and Sokal & Rohlf (1969).

Air temperature near ground level and sand temperature at about

1 cm depth were recorded during the observation period, as were other weather data.

Night feeding

Attempts were made to investigate the percentages of birds involved in night feeding and feeding rates at night. Note was made of whether birds appeared to continue feeding as night fell and attempts were made to view birds against moon-light reflected on the mud and pools. On the darker nights hand lamps and car head-lamps were used to investigate the presence of birds on the flats although little information was available from this method on whether the waders were feeding. Attention was also paid on all occasions to the occurrence of calls but these again did not give definite information on the activities of the birds. Although some relevant information was obtained, none of these methods was particularly satisfactory.

An image-intensifier, a night-viewing apparatus, was used on three nights in December 1974 (courtesy of the Institute of Terrestrial Ecology) and on three nights in February, six in March and several in May to July 1976 (courtesy of the Home Office Special Equipment Unit, Durham Police Headquarters). This equipment was very satisfactory for the detection of birds at a range of up to several hundred metres, provided that the ground was reasonably wet; however the contrast between bird plumage and dry sand was insufficient for detection except at fairly short range. The equipment had the disadvantage of heavy weight (it was only just portable by a person and was normally used from a vehicle on the sand flats) and very low magnification. In good conditions I was able to measure pecking rates, number of paces between waiting positions and prey captures and other aspects of foraging of Grey Plovers on the sand flats, but not of the smaller Ringed Plovers. Prey could not be identified, except for a few thin worms. Some measurements of the foraging performances of adult and chick Ringed Plovers at close range on the North Shore in the breeding season were made.

Invertebrate distributions and densities

A survey, with samples taken on a square grid at 50 m intervals in areas of high density and 100 m intervals elsewhere, was conducted

in May-June 1975 over my main study area on HIS by three undergraduate students (A.P. Coverdale, J.A. Hall & A.J. Wallis) under my direction. Four samples each 10 x 10 x 10 cm were taken at the corners of a 1 m square at each station, and were sieved through a 1 mm sieve in the field. Animals in each sample were brought back to the laboratory for identification and counting. The results are shown in Figure 3.

Variations in invertebrate density over the winter

To investigate variations in invertebrate density over the winter two 100 m x 100 m sampling areas were established, area B on the 'Grey Plover Flats' and area D at Godwit Creek' (Fig. 3). Within each area 36 stations on a 20 m x 20 m grid were marked using $\sqcap$ - shaped pieces of galvanised wire pushed into the mud so that they were flush with the surface and unlikely to affect flow and sedimentation patterns.

In November 1974 a single sample 10 cm x 10 cm x 30 cm depth was collected from a point 1 m south of each grid mark. Sampling to 30 cm depth included almost all invertebrates occurring commonly in this part of the mudflats except large *Arenicola*. The samples were transferred to polythene bags and kept outdoors until the following day when each sample was washed through a sieve of 20 meshes per inch (holes approximately squares of side 0.9 mm). Washing through a sieve of 30 meshes per inch (sides 0.5 mm) took considerably longer but retained very few additional animals. Examination of the washings, through both sieves, revealed no macrofauna. Retained material from each sample was washed into an enamel tray and all animals were picked from this and stored in a jar of sea water until the following day when they were sorted and counted. The shell lengths of a sample of molluscs were measured but measurements of worms were impracticable because of damage during sieving.

Sampling was repeated in February and May 1975 at stations making an equilateral triangle of side $\frac{1}{2}$ m with the November station (Fig. 4). This design allowed paired comparisons between sampling occasions in an attempt to prevent the generally high variance in densities over even a small area of mud-flat hiding seasonal changes. The data were analysed by two-way analysis of variance for paired comparisons (see

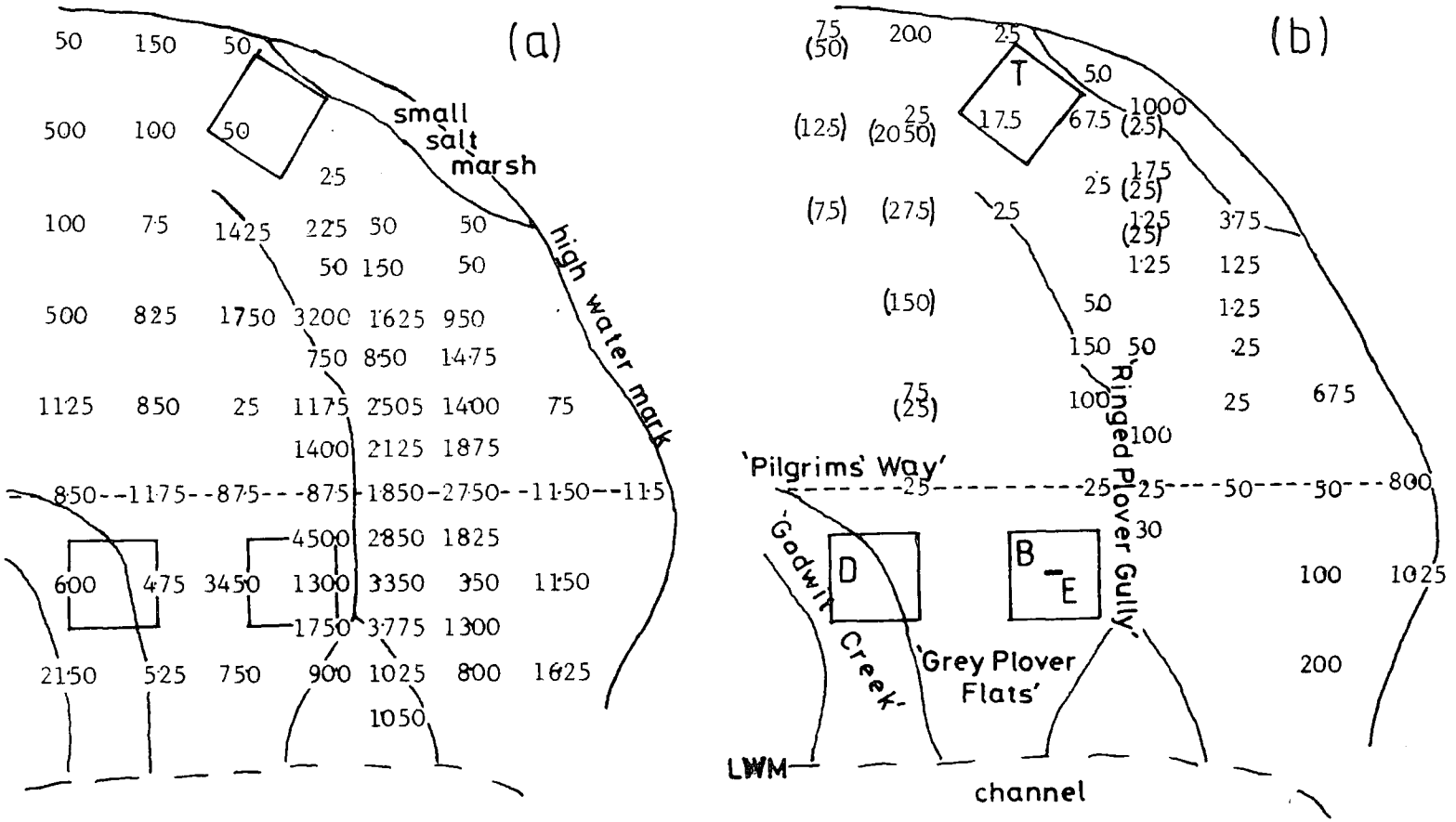


Figure 3. Densities (numbers per metre) of (a) thin red worms (mainly *Notomastus* and *Scoloplos*) and (b) *Bathyporeia* and *Hydrobia* (in parentheses) on eastern Holy Island Sands.

Main features are named and areas of seasonal sampling (B,D,T) and site of exclosure experiment (E) labelled.

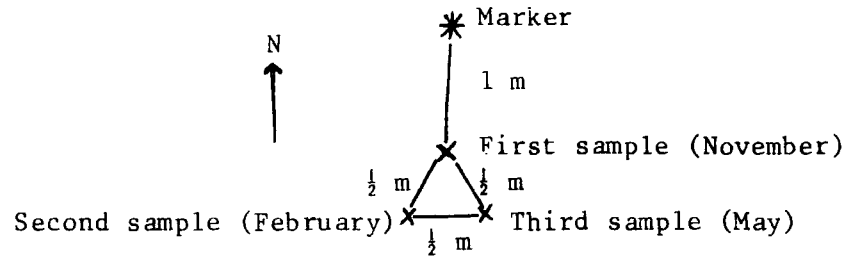


Figure 4. Arrangement of sampling at each grid station during investigation of seasonal variation.

Note: For more frequent sampling, the pattern could be extended to give up to seven occasions, six forming a hexagon around the initial site. The sample for any one date would then be equidistant from that of the previous date and the initial one.

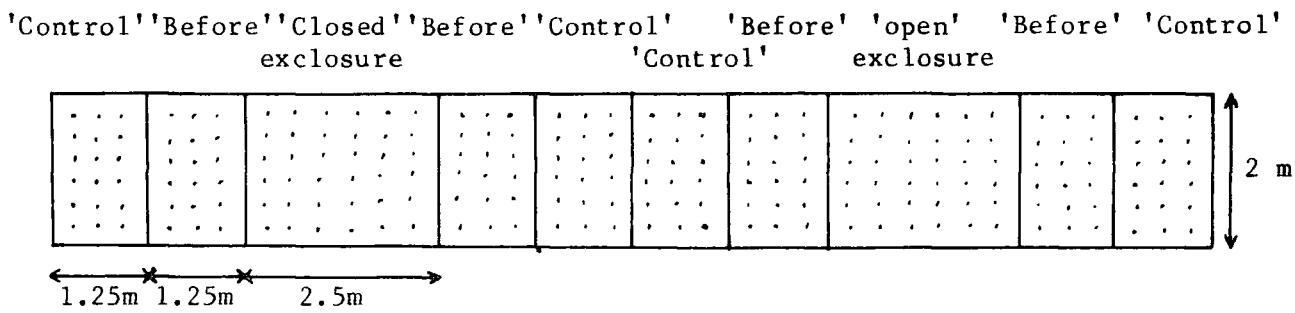


Figure 5. Arrangement of exclosures and adjacent sampling areas. Dots indicate sampling positions.

Sokal & Rohlf 1969, Box 11.3). All 36 stations were sampled in area B. Only the eastern 24 stations in area D were sampled in November and one sample was spilt during transportation on another occasion so that the analysis of variance for this area is based on a sample of 23 or 36, depending on the comparison. When mean densities for area D are given, these are based on the 23 stations common to all dates.

In February and May a similar sampling procedure was carried out in one 100 m x 100 m square on each of the upper sand flats on Holy Island Sands (Fig. 3) and on the N. Shore.

Exclosure experiment

In an attempt to investigate the effects of predation by birds and fishes on the invertebrates, two exclosures were established on 7 December 1974 on the mud-flats at approximately mid-tidal level and the mid level of area B. Each was built of wood of approximately 1 inch (2.5 cm) square section and consisted of a rectangle 2.5 x 2 m, supported at each corner by a wooden leg 30 cm high. Each leg was fastened to an angle-iron of length 6 ft (1.8 m) which had been driven into the mud.

One exclosure was covered with galvanised wire netting. It was postulated that this would exclude both birds and fish while the other exclosure, which was not covered with wire, would exclude only birds. Frequent observations over the winter confirmed that birds did not enter the exclosures but fed in the area between and adjacent to them. Observations on fish behaviour were not possible.

The exclosures were positioned as indicated in Figure 5 at approximately the same tidal level and as close as practicable given the requirements of the experiment. Once the exclosures had been placed on the flats but before the anchoring angle-irons were driven into the ground, eighteen 10 x 10 x 15 cm samples were taken in a regular, evenly spaced pattern from areas 1.25 m x 2 m immediately on each side of each exclosure as indicated in Figure 5. These samples were treated as indicated in the previous section.

During the period while the exclosures were in place a little

erosion of sediment was apparent particularly close to the legs of the exclosures. Also debris tended to collect and algae to grow on the structures, especially the 'closed' one, although this was removed as frequently as possible.

On 6 May 1975, 36 evenly spaced samples were taken from the area inside the 'open' exclosure and a further 18 from each of two areas 1.25 m x 2 m on either side of the initial sampling area (Fig. 5). On 16 May 1975, the 'closed' exclosure was removed and a similar sampling procedure carried out. The results were examined using analysis of variance.

Calorific contents

Thin red worms were collected from samples of the substrate in the main plover feeding area by hand sorting (as the worms are broken by sieving) and measured initially in an unstretched state and then by stretching until the worms broke. The relationship between stretched and unstretched length was:
stretched = 1.52 x unstretched + 2.5 ($r = 0.86$, $P < 0.001$).

Worms were separated according to their stretched length into classes corresponding to the bill height classification used in the field. No attempt was made to remove the sand adhering to the worms, partly because the plovers did not usually wash the worms taken, but mainly because cleaning would have caused further damage and possible loss of flesh. The samples were dried in a vacuum oven at 60 ^{o}C and then weighed.

Calorific values of the resulting dried material were obtained using a 'Durham' miniature bomb calorimeter (Phillipson 1964). No significant differences in calorific values were found between samples taken in early February and late March, and data from the two periods were combined. Smith (1975) found no significant difference between the calorific values of samples of *Arenicola* and thin red worms collected at Lindisfarne in September, December and May.

Determinations of calorific value were also made for *Bathyporeia*, sandhoppers *Talitrus saltator*, shore-flies, mainly

Coelopa, and tails of *Arenicola*. For the latter, tails 1 cm long were used as this was the approximate length seen to be taken by both Ringed and Grey Plovers in the field.

Impact of the birds on their prey

On seven occasions between each period of invertebrate sampling, areas B and D were observed during their periods of tidal emersion. On each occasion the numbers of all bird species present and feeding were counted at 15 minute intervals and in the intervening periods measurements of feeding rates of plovers were taken.

For each hour of tidal exposure the mean number of birds of each species feeding in each area was calculated for the seven dates within each inter-sampling period. These values were summed over the time of tidal exposure to give the number of bird-minutes of feeding per daylight tidal exposure.

Three rates of taking thin red worms per minute were calculated for each plover species in each inter-sampling period. These three rates were estimates of (i) the number of thin worms (i.e. observed thin worms plus the fractions of successful pecks with unknown prey and pecks with unknown outcome indicated by Table 1) taken per minute; (ii) the minimum number of thin worms (i.e. only those recorded as thin worms) taken per minute; and (iii) the maximum number of thin worms (i.e. thin worms plus pecks with unknown prey plus pecks with unknown outcome) taken per minute. As for each species each rate did not differ significantly between areas B and D the same values for the three estimates were used for both areas.

These three rates were multiplied by the relevant bird-minutes of feeding per daylight tide and the 92 days between each sampling occasion to give estimates of the number of thin worms taken in daylight from each area by each species during the two inter-sampling periods. Estimates were also made for Bar-tailed Godwits using the remarkably constant figure for rate of taking thin worms over various ranges of conditions and temperatures from -1 ^{o}C upwards reported by Smith (1975). No rate of capture of thin worms was available for Dunlins, the fourth species feeding commonly in these areas, because

of its tendency to swallow prey without removing its bill from the substrate. Bird-minutes of feeding of Dunlins are, however, given later with those of the other species. It is possible that much of the prey of this species consisted of meiofauna, as has been shown at Teesmouth (Evans *et al.* 1979). Other shorebird species were recorded in only very small numbers in the areas and were seen generally to take prey other than thin worms.

Food intake of the birds during daylight

The calorific values in Table 7 were used to convert the numbers of prey taken of each type to their energetic equivalents. A value of 2.5 cal per item was assumed for small prey as this approximates to the values of the smallest category of worms and of the small crustacea. Successful pecks with unknown prey and pecks with unknown outcome were allocated to small prey and small worms in the proportion indicated in Table 1. The small worms reallocated from these categories were assumed to consist of equal numbers of $< \frac{1}{4}$ bill-height worms and $\frac{1}{4}$ bill-height worms, as indicated by the ciné film analyses. Changes (even of about 100% for Ringed Plovers and larger for Grey Plovers) in the size of these assumed values have little effect on the results. The energy intakes from all prey taken over each observation period (usually 1 - 2 minutes) were summed and a mean rate of energy intake per minute was calculated for each hour for each set of tidal and weather conditions for which data on percentages of birds feeding were available (see below). In no case did mean rates of energy intake vary consistently or significantly during the tidal cycle. Therefore an overall mean rate was calculated for each set of weather conditions. (The main variations in hourly intake rate were due to the occasional *Arenicola* captured and these were taken too infrequently to give a consistent tidal pattern.)

At approximately 15 minute intervals the proportion of birds feeding (rather than loafing, preening, resting, etc.) was noted and an average value calculated for each hour of the tidal cycle. This measure of the average amount of time a bird spends feeding assumes that feeding and non-feeding birds were equally visible, and this is thought to have been reasonably true in the areas used in my study, namely open flat areas without deep creeks, vegetation or large rocks.

Spring ($\geqslant$ 11.9 m depth at high water over the New Entrance Lock Sill at Leith) and neap tides ($\leqslant$ 11.8 m) were treated separately; in local terms neap tides did not cover the entire area of HIS whereas spring tides did.

Because of the mobility of the birds and their scattered dispersion while feeding, it was rarely possible to obtain a full set of data from reasonable sample sizes of birds in a single day, so that most estimates are combined from two or more days. Separate estimates were made for each month and, when sufficient data were available, for different weather conditions in each month. For Ringed Plovers, juveniles were treated separately from adults in early autumn when they were fairly readily distinguishable in the field by plumage criteria.

For each set of conditions the mean proportions of birds feeding ("Feeding Intensity" FI) were plotted against time since high water. The area under the curve so produced (i.e. the average percentage of time spent feeding per daylight tidal cycle - "Percentage Feeding Time" PFT) was assessed by weighing on a suitably sensitive balance tracings of the graph on paper of uniform thickness. Each estimate of PFT was based on the equivalent of at least a full tidal period of observations and in many cases, because of overlap in combining data from several days, the equivalent of about two such periods.

The duration of daylight on the middle day of each month was calculated from tables for latitude 56^{o}N (*Whitaker's Almanac*). The periods of civil twilight were included in the total daylight period. This seemed appropriate as judged by general observation of bird behaviour; feeding rates and behaviour patterns did not change until light intensity was low.

The estimates of PFT, daylight duration and rate of energy intake were combined to give an average amount of food ingested per daylight period for each month and set of conditions. The daylight feeding duration was not corrected to allow for timing of high water (when feeding may be restricted) in relation to daylight. This was because the calculations concerned monthly averages and, at Lindisfarne, high water occurs in daylight at about the same frequency during both

spring and neap tides. It is, however, true that on certain days in winter birds will have less feeding time available than on others because of the occurrence of high water in daylight but the present data cannot examine this, because of the impossibility of obtaining a full set of data in daylight on a single day in mid-winter, exacerbated by the mobility of the birds.

The estimated food intake in daylight concerned an 'average' individual bird. Clearly, this method concealed individual variation in feeding rates and feeding time and the following of several identifiable individuals would have been preferable. This had been the original intention for Ringed Plovers, some of which were marked with colour rings, but the large feeding area utilized, the small size of the birds and the rings, their wide-ranging behaviour and the viewing conditions prevented this.

Basal metabolic rates of the plovers were estimated (from lean body weights) using the formula for non-passerines calculated by Lasiewski & Dawson (1967).

RESULTS

Diet

Details of prey recorded in the field, arranged by species, main parts of the study area and month, are given in Appendix 1 and summarized over the whole season in Table 2. No variation in diet between spring and neap tides was apparent. Table 3 allocates "successful pecks, unknown prey" to worms and other small prey and "pecks, unknown outcome" to worms, other small prey and failures in proportions indicated by data in Table 1. The numerical importance of thin worms to both species is clear.

The composition of thin worms by colours as assessed by examination of ciné film is given in Table 4. The greater variety on the North Shore is probably a result of the more diverse habitat covering a steeper range of tidal levels and shore types, including rocks and more weed, and also embracing midsummer conditions when a wider variety of invertebrates may be available to predation (see Paper 2).

TABLE 2. SUMMARY OF PREY IDENTIFIED DURING FIELD OBSERVATIONS

	GREY PLOVERS			RINGED PLOVERS			
	Low flats	High flats	Other areas	Low flats	High flats	N Shore	Other areas
Total pecks	2266	1318	183	4899	2814	4622	1615
Prey of which all sizes should be visible:	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)
Arenicola (whole)	26(1.2)	44(3.3)	3(1.6)	4(0.1)	7(0.3)	34(0.7)	6(0.4)
Arenicola (tails)	8(0.4)	9(0.7)	0(0)	5(0.1)	28(1.0)	10(0.2)	1(0.1)
Ragworms (probably *Nereis*)	1(0.04)	0(0)	0(0)	0(0)	0(0)	0(0)	2(0.1)
Crabs	3(0.1)	3(0.2)	2(1.1)	0(0)	1(0.04)	1(0.02)	0(0)
Algae	24(1.1)	52(4.0)	1(0.6)	14(0.3)	9(0.3)	15(0.3)	0(0)
Prey of which not all sizes visible:							
Thin worms (principally *Notomastus*)	788(34.8)	308(23.4)	27(14.8)	1063(21.7)	112(4.0)	512(11.1)	66(4.1)
Mollusca (*Macoma, Hydrobia, Littorina*)	21(0.9)	26(2.0)	1(0.6)	3(0.1)	2(0.1)	4(0.1)	0(0)
Diptera	0(0)	0	0(0)	0(0)	0(0)	9(0.2)	3(0.2)
Sandhoppers	0(0)	0	0(0)	0(0)	3(0.1)	2(0.04)	7(0.4)
other Crustacea	7(0.3)	1(0.1)	0(0)	11(0.2)	5(0.2)	22(0.5)	1(0.1)
*Successful pecks: prey not identified	540(23.8)	340(25.8)	55(30.1)	1537(31.4)	1143(40.6)	1415(30.6)	722(44.7)
Unsuccessful pecks	1(0.04)	3(0.2)	0(0)	1(0.02)	1(0.04)	1(0.02)	0(0)
*Pecks of unknown outcome	847(37.4)	532(40.4)	94(51.4)	2261(46.2)	1503(53.4)	2597(56.2)	807(50.0)

*These categories are allocated in Table 3 in accordance with data in Table 1.

TABLE 3. SUMMARY OF DIET OF RINGED AND GREY PLOVERS

Based on Table 2 with unidentified prey and pecks with unknown outcome allocated to thin worms, small prey and unsuccessful in accordance with data in Table 1.

	GREY PLOVERS			RINGED PLOVERS			
	Low flats	High flats	Other Areas	Low flats	High flats	N. Shore	Other areas
	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)	no.(%)
Arenicola (whole)	26(1.2)	44(3.3)	3(1.6)	4(0.1)	7(0.3)	34(0.7)	6(0.4)
Arenicola (tails)	8(0.4)	9(0.7)	0	5(0.1)	28(0.1)	10(0.2)	1(0.1)
Ragworms (probably *Nereis*)	1(0.04)	0	0	0	0	0	2(0.1)
Crabs	3(0.1)	3(0.2)	2(1.1)	0	1(0.04)	1(0.02)	0
Algae	24(1.1)	52(4.0)	1(0.6)	14(0.3)	9(0.3)	15(0.3)	0
Thin worms (principally *Notomastus*)	1771(78.2)	926(70.3)	133(72.7)	3162(64.5)	1574(55.9)	2731(59.1)	911(56.4)
Mollusca (*Macoma, Hydrobia, Littorina*)	21(0.9)	26(2.0)	1(0.6)	3(0.1)	2(0.1)	4(0.1)	0
Diptera	0	0	0	0	0	9(0.2)	3(0.2)
Sandhoppers (principally *Talitrus*)	0	0	0	0	3(0.1)	2(0.04)	7(0.4)
other Crustacea	7(0.3)	1(0.1)	0	11(0.2)	5(0.2)	22(0.5)	1(0.1)
various unidentified small prey	283(12.5)	178(13.5)	30(16.4)	1197(24.4)	851(30.2)	1217(26.3)	505(31.3)
(unsuccessful pecks)	121(5.3)	76(5.8)	13(7.1)	502(10.3)	334(11.9)	577(12.5)	179(11.1)

TABLE 4. COLOUR OF THIN WORMS TAKEN

numbers observed on ciné-film with percentage composition given in parentheses

	red	colourless	black or grey	white	yellow	total examined
GREY PLOVERS						
Low flats	185 (92)	1 (0.5)	14 (7)	1 (0.5)		201
High flats	70 (100)					70
RINGED PLOVERS						
Low flats	204 (96.7)	4 (1.9)	3 (1.4)			211
High flats	33 (97.1)		1 (2.9)			34
North Shore	31 (75.6)	2 (4.9)	4 (9.8)	1 (2.4)	3 (7.3)	41

Sampling of the sand for potential prey indicates that the red worms are the capitellid polychaete *Notomastus latericeus* and the ariciid polychaete *Scoloplos armiger*. Because of variation in pigmentation, the apparently clear and black worms may also be of this species. The yellow worms may be *Phyllodoce maculata*, which was found at moderate densities in the study area during the various invertebrate samplings.

Analyses of sizes of thin worms are given in Appendix 2 and summarized in Table 5. The sizes of *Scoloplos* found in the area indicate that these are likely to contribute significantly only to '< ¼ bill-height worms' and '¼ bill-height worms' and that larger red worms are almost entirely *Notomastus*; however, the latter also contribute to the smallest categories of worms. Table 5 does not include those worms initially categorized in Table 2 as "small prey" and "pecks" before correction. These are almost entirely '< ¼ bill-height worms' and '¼ bill-height worms'.

Numerically the second most important group of prey are the 'various small' items. Although these probably include further thin worms and fragments of these, the other small items identified give some clue to the other species involved. Sandhoppers, mainly *Talitrus saltator*, and Diptera (chiefly Coelopids) are important to Ringed Plovers particularly in the breeding season when these are feeding on the wrack line. On the sand flats various small molluscs were seen to be taken and comparison of the shapes of these and the potential prey species found by substrate sampling indicated that most were the prosobranch *Hydrobia ulvae*, the tellin *Macoma balthica* and, less frequently, the winkle *Littorina* sp. On one occasion when a Ringed Plover was observed feeding at very close range it was seen to take part of a syphon of a *Macoma*. This type of prey may have been much more frequently taken as *Macoma* siphons were seen to be extended and actively feeding in some water-filled hollows (such as depressions over *Arenicola* head-tubes) while the tide was low.

Small Crustacea probably formed many of the "small prey" especially at higher tidal levels. This assessment is based on (i) those few observed to be taken, (ii) the species found to be present

TABLE 5. SUMMARY OF SIZES OF THIN WORMS SEEN TO BE TAKEN

length in relation to height of bill off ground	GREY PLOVER stretched length (cm)	Low flats	High flats	Other	RINGED PLOVER stretched length (cm)	Low flats	High flats	North Shore	Other
< ¼ bill height		281(38.2)	178(68.2)	22(84.6)		495(48.3)	65(63.1)	298(65.6)	52(88.1)
¼ " "		141(19.2)	14(5.4)	1(3.9)		75(7.3)	9(8.7)	29(6.4)	1(1.7)
½ " "	6	152(20.7)	33(12.6)	1(3.9)	4	133(13.0)	16(15.5)	68(15.0)	5(8.5)
¾ " "		42(5.7)	8(3.1)	0(0)		49(4.8)	3(2.9)	6(1.3)	1(1.7)
1 " "	12	62(8.4)	22(8.4)	0(0)	8	157(15.3)	10(9.7)	47(10.4)	0(0)
1¼ " "		35(4.8)	6(2.3)	0(0)		29(2.8)	0(0)	3(0.7)	0(0)
1½ " "	18	19(2.6)	0(0)	2(7.7)	12	53(5.2)	0(0)	3(0.7)	0(0)
1¾ " "		2(0.3)	0(0)	0(0)		4(0.4)	0(0)	0(0)	0(0)
2 " "	24	2(0.3)	0(0)	0(0)	18	25(2.4)	0(0)	0(0)	0(0)
>2 " "		0(0)	0(0)	0(0)		5(0.5)	0(0)	0(0)	0(0)
Total		736	261	26		1025	103	454	59

by inspection and sampling in the areas in which plovers were feeding, and (iii) considerations of the birds' behaviour (see Paper 2). The main species concerned were probably the amphipod *Bathyporeia pelagica* and the isopod *Eurydice pulchra*.

In other areas of the reserve, *Nereis diversicolor* was a main prey of Grey Plovers, especially on Fenham Flats. In spring flocks of Ringed Plovers also fed on concentrations of *Eurydice pulchra* on the very high flats near the Sand Rig and on *Corophium volutator* below the salt marsh on Beal Sands, near the bridge and Causeway (Fig. 1). In late summer many Ringed Plovers fed on concentrations of small red worms, believed to be newly-settled *Scoloplos*, at Guile Point.

Table 8 combines the prey composition (Table 3), the size composition of thin worms and *Arenicola* (Tables 4 & 6), and the measured calorific values (Smith 1975 for *Arenicola*, Joffe (unpublished) for *Nereis*, Table 7 for other items) to assess the relative energetic contributions of the various prey types. 'Small items' are given the calorific value of 2.5 cal/item (see Methods). Small changes to this assumed value would clearly not greatly change the picture in Table 8. However this figure is not really suitable for the North Shore and 'other areas' because of the predominance there of Diptera and sandhoppers. These areas are therefore omitted from Table 8.

Table 8 demonstrates the importance in energetic terms of the relatively small number of *Arenicola* to Grey Plovers and the very small contribution of "small prey" to this species. Thin worms are fairly important to Grey Plovers and remain the most important prey for Ringed Plovers in energetic as well as numerical terms. The very small number of *Arenicola* and the very large number of small items are both of secondary importance to this species.

Night feeding

Observations of waders as night fell suggested that, as found in the same area by Smith (1975) and at Teesmouth by Knights (1979), birds tended to leave the high-tide roost later after HW at night

TABLE 6. SIZES OF *ARENICOLA* TAKEN

	GREY PLOVERS			RINGED PLOVERS			
length in relation to height of bill off the ground	length (cm)	Low flats	High flats	length (cm)	Low flats	High flats	North Shore
< ¼ bill height		2	4		1	0	1
¼ " "		2	3		0	0	0
½ " "	6	6	4	4	1	1	5
¾ " "		6	5		0	0	4
1 " "	12	19	7	8	0	0	6
1¼ " "		1			0	0	1
1½ " "	18	3		12	0	0	
>1½ " "					1	1	

TABLE 7. CALORIFIC VALUES ESTIMATED

	stretched length (mm)	cal/ animal	number weighed	number calorific determinations
small thin worms (= *Scoloplos*)		2.64	14	1
thin worms (*Notomastus*)				
¼ RP bill height	10 - 30	6.45	37	
½ " " "	30 - 50	10.25	41	
¾ " " "	50 - 70	14.47	12	
1 " " "	70 - 90	16.57	9	12
¼ GP " "	15 - 45	7.34	41	
½ " " "	45 - 75	14.67	11	
¾ " " "	75 -105	17.65	7	
(larval worms		0.43)	10	
Bathyporeia		2.18	10	1
Arenicola tails		53.07	3	4
sandhopper *Talitrus*		26.85	10	3
shore fly *Coelopa*		9.45	12	1

Average calorific value of whole *Arenicola* taken, weighted by proportion in each of Smith's (1975) size classes:

by Grey Plover	973
by Ringed Plover	575

TABLE 8. RELATIVE CONTRIBUTIONS (% OF TOTAL ENERGY INTAKE) TO THE DIET OF PLOVERS AT LINDISFARNE BY VARIOUS CATEGORIES OF PREY.

	GREY PLOVERS		RINGED PLOVERS	
	Low flats	High flats	Low flats	High flats
Whole *Arenicola*	62.8	83.2	12.6	29.5
Arenicola tails	1.1	1.0	1.2	9.1
Ragworms	0.2	0	0	0
Crabs	5.4	5.2	0	6.8
Thin worms (*Notomastus*, *Scoloplos*)	29.1	10.0	75.5	44.3
Small prey	1.3	0.7	10.7	10.3

than by day and possibly also to return to roost earlier on the rising tide. Observations of the presence of birds on the flats also suggested that, on moon-lit nights, birds delayed the move from roost to feeding areas until the moon rose, but this was difficult to quantify. The tendency to delay the start of feeding or, if already feeding, to stop early at night appeared strongest up to October and from March and weakest between November and February.

Observations during the main part of the night were made fairly regularly from late October 1974 to January 1975 and January to August 1976 using either moon-light or an image-intensifier. On four nights from the end of October to late January when there was little or no wind, Grey and Ringed Plovers and other species were observed feeding on the sand flats at fairly high densities, which I assessed as similar to those observed in daytime (Table 9). (Because of the different viewing conditions, by day and night, it was not possible to make quantitative comparisons.)

High winds on three nights in mid-winter appeared either to keep birds from the feeding areas or to depress the proportions of birds feeding or the time spent feeding by individuals. Gale force winds and freezing temperatures occurred on the night of 12 December 1974 and no birds were observed on the flats. On the following night, when the wind had dropped somewhat but was still strong, few birds were seen feeding. On the following night, when the temperature remained below zero but the wind had dropped to light, numerous plovers of both species and other waders were feeding on the flats. On 20 January 1976, with wind force 8, Grey and Ringed Plovers and Dunlins were present in fairly high numbers on the sand flats but few were feeding and many roosted.

On three nights of light wind in February (temperature about 2-3 ^{o}C), Grey Plovers and other waders were observed feeding at night but never at densities as high as by day (nor as high as on nights of light wind earlier in the winter when nights were longer and temperatures lower).

Observations were made on six nights in March (temperatures 2 ^{o}

TABLE 9. SUMMARY OF OBSERVATIONS ON THE FEEDING GROUNDS AT NIGHT IN WINTER

Date	Intensifier used	Wind-force	Temp. (°C)	Light conditions	Birds observed on HIS
30.10.74		2	5	full moon, cloud cover, fairly light	Waders, including Grey and Ringed Plovers feeding in about the same numbers as by day
12.12.74	I	8	<0	new moon, overcast, dark	No birds seen
13.12.74	I	6	<0	" " " "	c70 Bar-tailed Godwits, c70 Dunlins & 2 Grey Plovers feeding
14.12.74	I	4	<0	" " " "	Waders, including Grey and Ringed Plovers, feeding in about the same numbers as by day
28.12.74		3	4	full moon,5/8 cloud	" " " " " " " "
1. 1.75		0	6	3/4 moon, 2/8 cloud	Many waders,including Grey Plovers,in area,probably feeding
20. 1.76		8	1	" " " "	Grey and Ringed Plovers and Dunlins on flats but mainly roosting and not feeding
4. 2.76	I	1	2	1/4 moon, fairly clear	Several Grey Plovers, Dunlins and Godwits feeding
5. 2.76	I	1	2	" " " "	4 Grey Plovers and several Dunlins feeding
7. 2.76	I	0	3	1/3 moon, clear but misty	Curlews, Godwits, Dunlins and Grey Plovers present, some feeding, many roosting
2. 3.76	I	3	3	new moon, clear sky	6 Grey Plovers, 10 Godwit, 1 Curlew feeding. Many Curlews, Godwits and probably Grey Plovers roosting
4. 3.76	I	3	3	new moon, misty, dark	A few Grey Plovers and Curlews feeding
5. 3.76	I	4	4	1/8 moon, clear but cloud developing	2 Grey Plovers, a few Ringed Plovers and Dunlins feeding, far fewer than by day
6. 3.76	I	8	2	moon completely hidden by cloud, dark	Very few birds found; 1 Curlew & 10 Dunlins feeding
12. 3.76	I	0	7	1/2 moon, overcast, but fairly light	Small numbers of Grey Plovers, Godwits, Curlews & Dunlins feeding; many resting
13. 3.76	I	0	7	" " " " "	" " " " " " " " "

to 8 °C). Small numbers of waders, including Grey Plovers and sometimes Ringed Plovers, were present on five occasions of fairly light wind but never at very high density and certainly many fewer than in daytime or at night earlier in the winter. On one night of force 8 winds, very few birds were seen.

On several occasions from May to August, no birds were seen feeding on the flats of HIS at night although Ringed Plovers, including locally breeding birds, and some other species, notably Black-headed Gulls, *Larus ridibundus* were seen feeding on the North Shore and Snook of Holy Island. In these latter cases, however, the prey appeared to consist entirely of sandhoppers Talidridae which are active mainly at night near high water mark.

On both occasions when a comparison was possible, Ringed Plovers pecked significantly faster in the daytime than at night (Table 10). The prey taken at night could not be ascertained except that, in June, some - and probably most - nocturnal prey consisted of sandhoppers and, in this situation, daytime prey may have differed somewhat, although sandhoppers were certainly included then (Table 2). (The calorific content of *Talitrus* is much greater than of *Eurydice* or *Bathyporeia*.)

Comparisons were also possible on two occasions for Grey Plovers. On a very dark, moonless night in February, the mean pecking rate was significantly lower than in daylight (Table 10). In March the mean pecking rate during a moonlit night was similar to that in daytime. Although most prey could not be identified, several thin worms were seen to be taken. No *Arenicola* were seen, although (because of their large size) any taken would have been visible in most situations. Further aspects of the foraging behaviour of the plovers at night are considered in Paper 2.

Seasonal variations in prey density

Three species were found abundantly on eastern HIS: *Notomastus latericeus*, *Scoloplos armiger* and *Macoma balthica*; the seasonal variations in densities of these are summarized in Table 11. As indicated above, the other common species of the macrofauna, the lugworm

TABLE 10. PECKING RATES OF PLOVERS AT NIGHT COMPARED WITH DAYTIME RATES IN THE SAME SITUATION

Species	Date	Area	Conditions	No. of cases	Total period of observation (sec.)	Mean total pecks per minute	s.e.	t	Significance
Ringed Plover	26. 2.75	N. Shore	just before sunset 3°C	7	689	17.0	2.93		
" "	"	"	just after sunset 3°C	10	417	7.3	0.84	3.78	**
Ringed Plover	17. 6.76	N. Shore	12°C through day	40	2311	17.5	1.54		
" "	"	"	11°C midnight	6	360	7.2	0.96	5.67	***
Grey Plover	7. 2.76	E. HIS	daytime 3°C	25	1737	8.2	0.65		
" "	"	"	night, no moon, clear sky 2.5°C	18	1470	4.1	0.64	4.30	***
Grey Plover	12. 3.76	E. HIS	daytime 6.5°C calm	33	2372	5.0	0.49		
" "	"	"	night, 7°C ½ moon, calm	6	437	4.9	0.73	0.11	n.s.

Arenicola marina, was normally too deep to be sampled by the technique used. Other species recorded, all at moderate to low frequency, were: *Phyllodoce maculata*, *Nereis diversicolor*, *Lanice conchilega*, *Nephthys hombergi*, *Cirratulus* sp., several small polychaetes and oligochaetes, *Cerastoderma edule*, *Tellina tenuis*, *Scrobicularia plana*, *Mytilus edulis*, *Littorina saxatilis*, *Bathyporeia pelagica*, *Gammarus* sp., *Corophium volutator*, *Eurydice pulchra*, *Urothoe* sp., and *Carcinus maenus*.

Mean densities of all three dominant species were higher in area B than area D, this possibly being related to the greater degree of tidal scouring in 'Godwit Creek' (D) than on 'Grey Plover Flats' (B). Neither *Scoloplos* nor *Macoma* showed marked changes of density between sampling occasions and neither did they show significant variation in density between stations. In contrast densities of *Notomastus* generally showed significant variation in relation to sampling stations and to season. In both areas, mean density fell significantly, by 31% in area B and by 90% in area D (which had a lower initial density). A slight further fall in mean density between February and May was not significant. Unfortunately, no information appears to be available on the life cycle of *Notomastus* or the timing of its reproduction.

The results from the exclosure experiment are given in Table 12. *Notomastus* densities were slightly but not significantly higher in both types of exclosures at the end than at the start of the experiment. The control areas had slightly, but not (or barely) significantly, lower densities than those found at the start of the experiment, but significantly lower densities than within the exclosures.

For *Macoma*, trends tended to be more marked in the closed than the open exclosure. Densities were significantly lower in the exclosures than both the initial and the 'control' situation, between which there were no significant differences.

Trends also tended to be more marked in the closed exclosure for *Scoloplos* but the pattern was not as simple. Densities were significantly lower in both exclosures after than before the experiment.

TABLE 11. CHANGES IN DENSITY OF ABUNDANT MACRO-BENTHOS ON EASTERN HOLY ISLAND SANDS IN WINTER 1974 - 75

	November Density	Anova Nov-Feb	February density	Anova Feb-May	May density	Anova Nov-May
Notomastus						
Area B	2244	25.30 ***	1550	1.30 n.s.	1397	24.40 ***
		3.50 ***		2.99 ***		1.96 *
Area D	678	13.14 **	65	0.01 n.s.	22	14.68 ***
		0.92 n.s.		1.96 *		1.00 n.s.
Scoloplos						
Area B	1275	5.36 *	994	0.17 n.s.	1042	3.07 n.s.
		1.69 n.s.		1.39 n.s.		0.68 n.s.
Area D	270	0.12 n.s.	239	0.05 n.s.	178	0.91 n.s.
		1.10 n.s.		1.21 n.s.		0.64 n.s.
Macoma						
Area B	567	1.37 n.s.	517	0.63 n.s.	553	0.05 n.s.
		3.13 n.s.		2.52 n.s.		1.05 n.s.
Area D	200	1.99 n.s.	117	1.53 n.s.	170	0.28 n.s.
		0.47 n.s.		1.67 n.s.		0.72 n.s.

Mean densities given as numbers m^{-2}, 'Anova' gives F values and significance levels. The upper figure relates to changes due to date and the lower one to differences associated with sampling sites (see Sokal & Rohlf 1969, Box 11.3). The mean densities are based on 36 samples in B and 23 in D.

TABLE 12. COMPARISON OF DENSITIES OF MACRO-BENTHOS ON HOLY ISLAND SANDS IN RELATION TO AN EXCLOSURE EXPERIMENT

Species	Type of exclosure	Before experiment[1]	F value before vs after	In exclosure after experiment[2]	F value after vs control	Control after experiment[2]	F value before vs control
Notomastus	open	1156	3.69 n.s.	1391	9.60 **	1011	1.40 n.s.
	closed	2253	0.77 n.s.	2383	8.36 **	1949	4.10 *
Scoloplos	open	1344	7.90 **	966	0.16 n.s.	1019	5.90 *
	closed	1231	18.52 ***	658	14.35 ***	1166	0.23 n.s.
Macoma	open	417	7.31 **	306	5.28 *	400	0.17 n.s.
	closed	442	15.81 ***	264	34.55 ***	529	3.73 n.s.

Mean Densities in numbers per metre^2.

F values calculated according to Sokal & Rohlf (1969).

[1] 7 December 1974

[2] 6 May 1975 for open exclosure; 16 May 1975 for closed.

Also, in the closed one, the density after the experiment was significantly lower than in the control area. For the open exclosure, density was significantly lower in the control area after the experiment than in the initial situation.

It is clear that the effect of the exclosures on the microenvironment overwhelmed any planned experimental effect. Such effects may include sedimentation and erosion, shelter, humidity and collection of organic material, particularly for the closed exclosure. Densities of *Macoma* and *Scoloplos* actually fell inside the exclosure while those of *Notomastus* may have risen slightly. This may reflect habitat preferences for more open situations by the former two. *Notomastus* is frequently found under algae covered patches on the flats. The fact that *Notomastus* densities fell less in the 'control' areas for this experiment than over the surrounding area (Table 11) may indicate that effects of the exclosures may extend some way from tham, either via physical conditions or by reducing bird predation near them. Although birds were commonly seen to feed near the exclosures, this was not quantified.

On the upper sampling area (T in Fig. 3) of HIS the amphipod *Bathyporeia pelagica* was the commonest species and several other amphipods and isopods, notably *Eurydice pulchra*, were also recorded. Worms including *Notomastus* occurred in small numbers. The density of *Bathyporeia* fell greatly and significantly from February to May (Table 13) and changes were also indicated by the data on less common species. However, as all the Crustacea are highly mobile and may move considerable distances when the tide is in, in some cases probably being drifted in the surface waters by winds, large variations are to be expected and do not necessarily indicate real seasonal changes. Some insect larvae were also recorded in May.

On the North Shore, a wider variety of species occurred fairly commonly, including several insect larvae and adults, and various other polychaetes and small Crustacea, in addition to many of those found in the flats. The commonest species, *Scoloplos* and *Macoma*, tended to occur at lower density than on the open flats (Table 13).

TABLE 13. CHANGES IN DENSITY OF ABUNDANT MACRO-BENTHOS NEAR HOLY ISLAND SNOOK IN WINTER 1974 - 75

	February density	Anova Feb-May	May density
North Shore			
Scoloplos	422	0.58 n.s.	364
		6.18 ***	
Macoma	686	0.10 n.s.	750
		2.08 *	
Near small saltmarsh			
Bathyporeia	1614	18.01 ***	556
		1.33 n.s.	

Notes as for Table 11.

The greater variation is probably related to the more varied habitat, with mud, sand, some stones and weed and the greater range of tidal levels. This is reflected in an high component of variance due to sampling stations. There were no significant changes in density of *Scoloplos* or *Macoma* between February and May. Insect larvae and sandhoppers Talitridae appeared in the samples in May.

Feeding durations and energy intake

The feeding intensities of the two plover speciesare shown in relation to season in Figures 6 & 7, and the resulting PFT's in Figure 8. For Ringed Plovers a comparison between juveniles and adults is possible in early autumn, the former generally feeding for longer periods than the latter.

For both Ringed and Grey Plovers, high water of spring tides generally prevented feeding activities because no feeding areas were available but in the cold period (1 ^{o} - 2 ^{o}C) in January, some Ringed Plovers contrived to feed on the high beaches over the high water period. The prevention of feeding around the time of high water reduced the maximum PFT generally possible from nearly 100% on neap tides to about 70% on most springs (the latter obviously somewhat dependent on the actual tidal height on the days of observation) (Figs. 6 & 7). In September, feeding on sandhoppers and wrack flies around high water allowed slightly higher PFT's. Possibly, this was not usually profitable in later months because of reduced numbers and availability of such prey.

In early autumn and spring FI's were generally well below 100% for much of the tidal cycle but in winter FI's remained at or near 100% throughout the observation periods or until spring high tides prevented feeding. On several occasions in winter FI's were depressed to zero, usually as a result of gusts of high wind or squally showers, e.g. on a day of neap tides in January with a temperature of 2.5 ^{o}C. The cessation of feeding at these times appeared not to result from the birds' seeking of shelter as they commonly spent the duration of the squalls, usually between 5 and 15 minutes, preening or bathing with fluffed-up feathers. Difficulty in locating prey seems a more likely cause (see Paper 2). Such squalls sometimes markedly affected

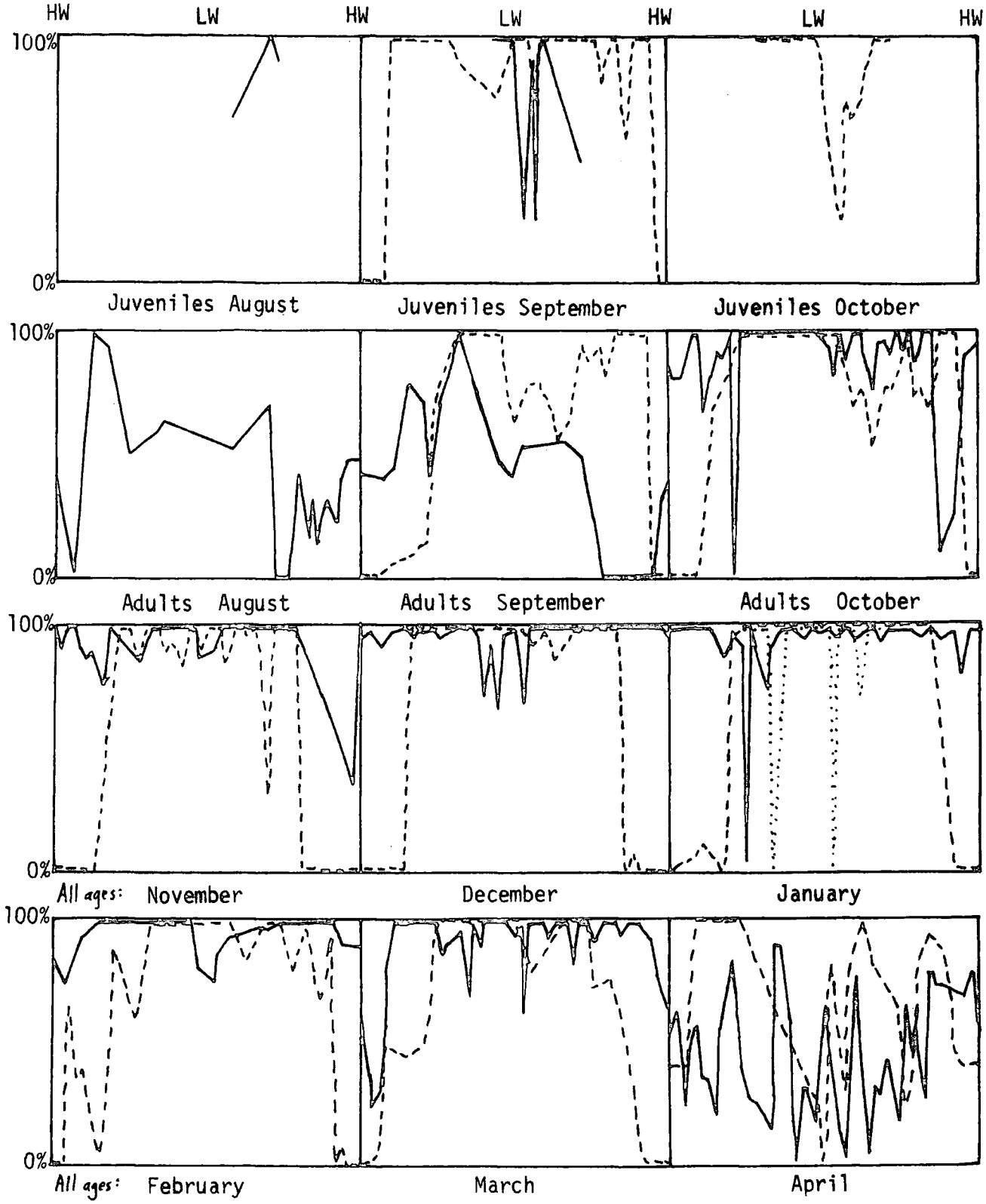


Figure 6. Example of feeding intensities of Ringed Plovers in relation to tide in different months.

——— neap ----- spring ····· depression of FI by squalls, January neap

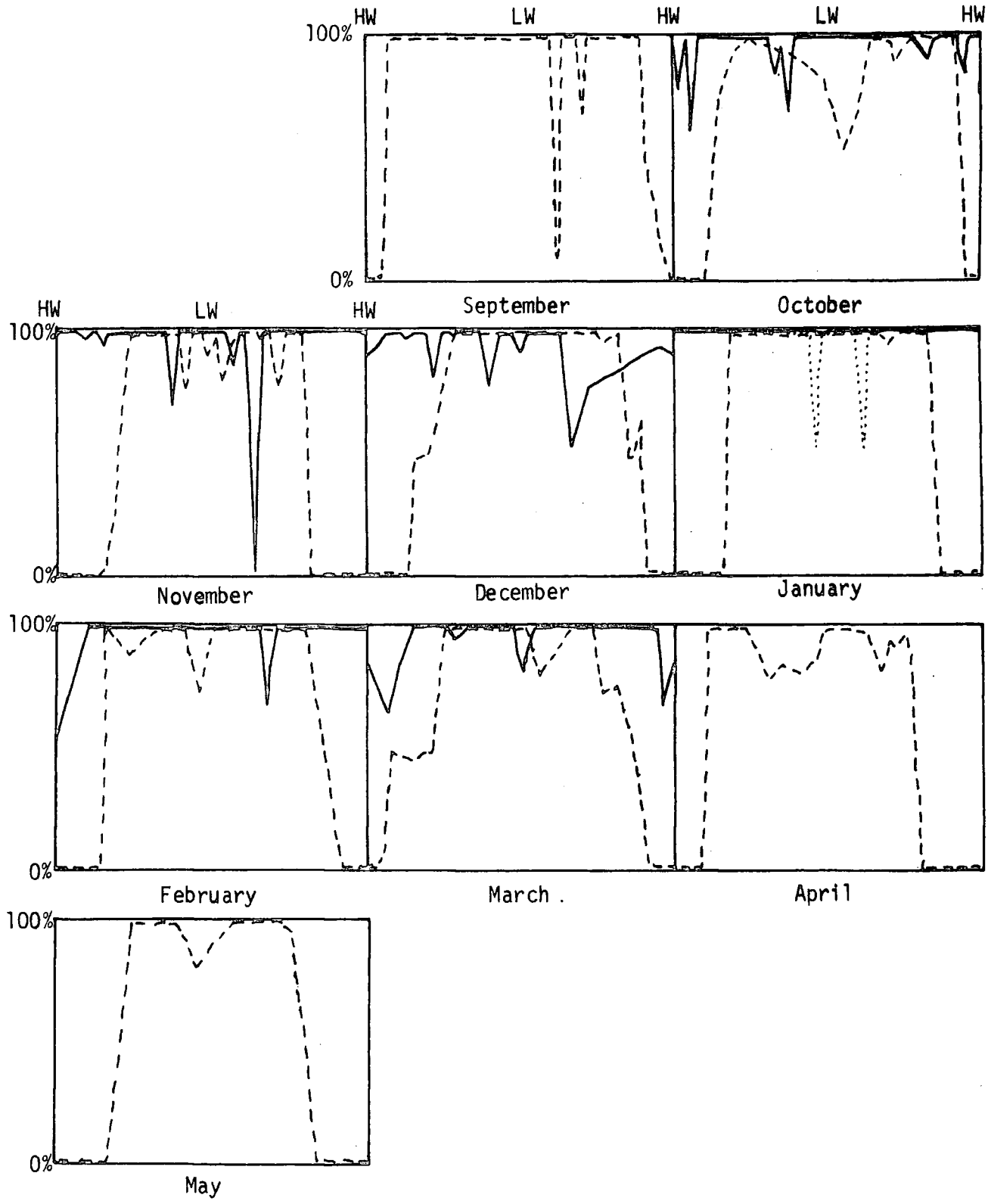


Figure 7. Examples of feeding intensities of Grey Plovers in relation to tide in different months. Legend as Figure 6.

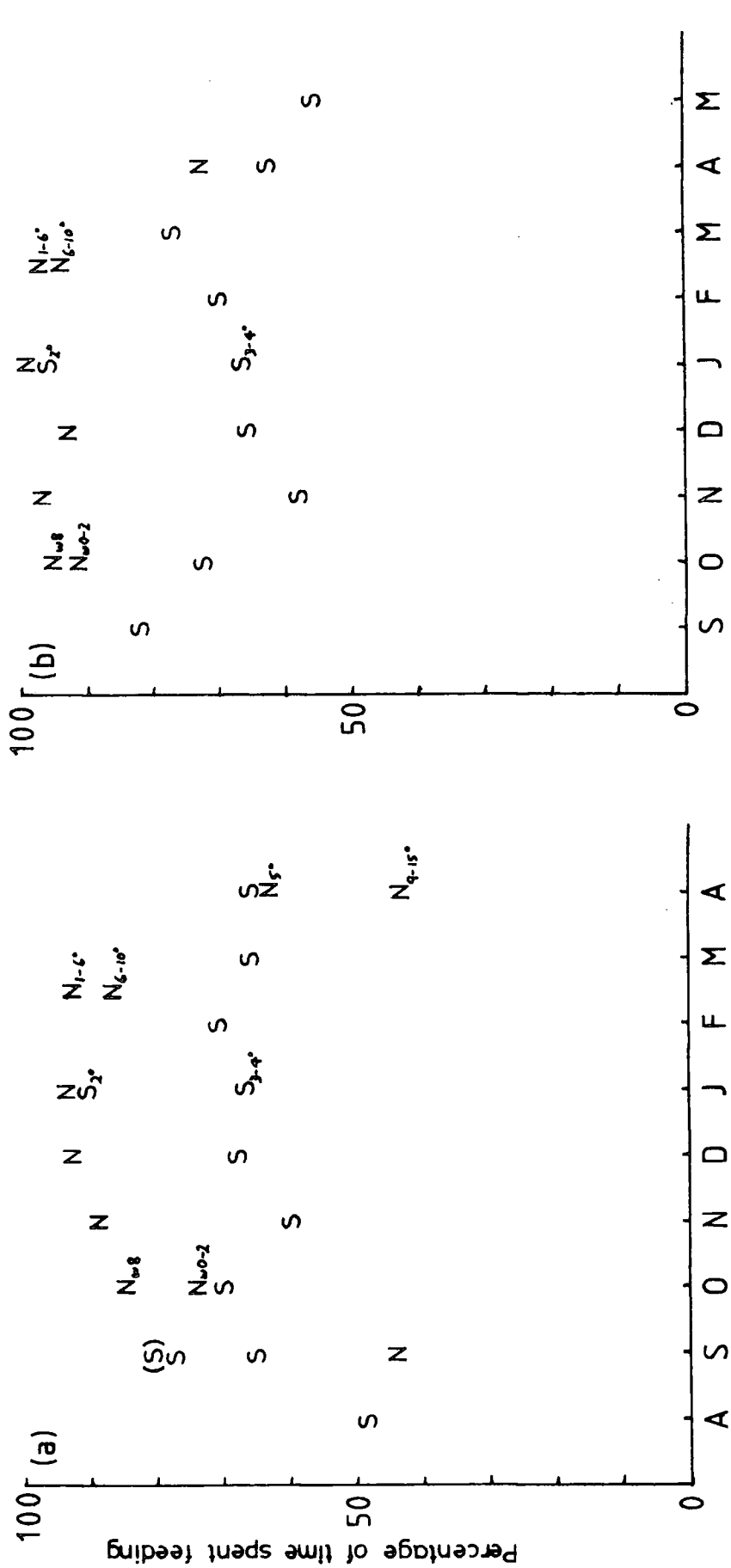


Figure 8. Percentage of time spent feeding by (a) Ringed Plovers and (b) Grey Plovers at Lindisfarne NNR in relation to season and various conditions.

S = spring; N = neap; (S) = juveniles; w = windforce; ^{o} = ^{o}C

TABLE 14. ESTIMATION OF DAYTIME CALORIFIC INTAKES OF RINGED PLOVERS AT LINDISFARNE IN VARIOUS CONDITIONS

	Percentage of time spent feeding[1]	Daylight period including civil twilight (min)	Feeding rate cal/min±s.e. (sample size)	Estimated daytime calorific intake (kcal)	Factor x BMR	Effect of increasing number of *Arenicola* taken[2]
Aug neap adults	48.8	946	98.9±21.66(45)	45.65	4.37	(4.89/ 25%)
Sep neap adults	44.0	800	73.8±15.02(8)	25.98	2.49	(4.66/ ∞ %)
Sep spring adults estimate 1	78.2	800	74.0± 8.57(16)	46.29	4.43	(4.61/ ∞ %)
Sep spring adults estimate 2	62.5	800	74.0± 8.75(16)	37.00	3.54	(3.69/ ∞ %)
Sep spring juveniles	80.1	800	126.4±48.20(10)	81.00	7.75	(10.35/100%)
Oct neap adults windforce 8	84.7	662	63.7± 4.69(27)	35.72	3.42	(4.14/100%)
Oct neap adults windforce 0 to 2	73.7	662	64.6± 4.81(25)	31.52	3.02	(3.77/ ∞ %)
Oct spring	70.3	662	62.7± 3.52(33)	29.18	2.79	(3.47/ ∞ %)
Nov neap	88.6	535	60.4± 5.54(19)	28.63	2.74	(3.98/ ∞ %)
Nov spring	59.5	535	71.0± 9.91(7)	22.60	2.16	(4.67/ ∞ %)
Dec neap	93.3	466	59.1± 3.46(23)	25.70	2.46	(3.35/ ∞ %)
Dec spring	68.1	466	51.5± 6.58(6)	16.34	1.56	(3.47/ ∞ %)
Jan neap	93.6	503	83.3± 7.97(109)	39.22	3.75	(3.93/ 25%)
Jan spring 3-4°C	66.6	503	87.1± 8.79(98)	29.18	2.79	(2.93/ 25%)
Jan spring 1-2°C	90.9	503	33.2± 4.45(23)	15.18	1.45	(2.41/ ∞ %)
Feb spring	71.1	617	47.1± 7.53(9)	20.66	1.98	(3.95/ ∞ %)
Feb-Mar neap 1-6°C	93.1	680	94.0±14.45(57)	59.51	5.69	(5.99/ 33%)
Feb-Mar neap 6.5-10°C	87.4	680	55.7± 4.59(94)	33.10	3.17	(3.46/100%)
Mar spring	66.5	748	110.6±54.62(33)	55.01	5.26	(5.83/ 25%)
Apr neap 5.0°C	64.4	896	78.4± 7.99(57)	45.24	4.33	(4.76/ 50%)
Apr neap 9.5-15°C	43.1	896	80.5±11.08(48)	31.09	2.97	(3.35/ 50%)
Apr spring	66.2	896	77.5± 8.56(43)	45.97	4.40	(5.13/100%)

Notes

[1]Each estimate of PFT is based on the equivalent of at least one full tidal cycle, usually more (see text). In September spring conditions, sufficient data were available for two separate estimates.

[2]To help estimate possible variation, the effect of adding one *Arenicola* to those observed in each weather condition/month on the intake is indicated (see text); given as (factor x BMR/% theoretical increase in *Arenicola* taken).

TABLE 15. ESTIMATION OF DAYTIME CALORIFIC INTAKES OF GREY PLOVERS AT LINDISFARNE IN VARIOUS CONDITIONS

	Percentage of time spent feeding[1]	Daylight period including civil twilight (min)	Feeding rate cal/min±s.e. (sample size)	Estimated daytime calorific intake (kcal)	Factor x BMR	Effect of increasing number of *Arenicola* taken[2]
Sep spring	81.4	800	151.5± 61.47(13)	98.66	3.87	(5.12/50%)
Oct neap						
windforce 8	96.4	662	57.1± 14.81(27)	36.44	1.43	(1.76/50%)
windforce 0-2	91.2	662	220.4±111.68(8)	133.07	5.22	(7.01/50%)
Oct spring	72.9	662	78.5± 28.17(18)	37.88	1.49	(2.10/50%)
Nov neap	96.9	535	33.9± 3.51(14)	17.57	0.69	(1.44/∞ %)
Nov spring	57.8	535	101.4± 49.81(10)	31.36	1.23	(1.97/100%)
Dec neap	93.2	466	140.8± 29.36(18)	61.15	2.40	(2.91/20%)
Dec spring	65.6	466	69.2± 64.28(46)	21.15	0.83	(0.99/50%)
Jan neap 2.7-5°C	99.7	503	62.8± 15.62(44)	31.49	1.24	(1.39/33%)
Jan spring 3-4°C	66.6	503	80.2± 28.88(23)	26.87	1.05	(1.45/100%)
Jan spring 1-2°C	96.6	503	26.9± 3.46(8)	13.07	0.51	(2.34/∞ %)
Feb spring	69.8	617	224.7± 67.41(22)	96.77	3.79	(4.11/10%)
Feb-Mar neap 1-6°C	96.8	680	171.4± 38.80(69)	112.82	4.42	(4.70/8.3%)
Feb-Mar neap 6.5-10°C	94.9	680	50.2± 13.48(4)	32.40	1.27	(5.25/∞ %)
Mar spring	76.7	748	173.5± 37.82(34)	99.54	3.90	(4.22/10%)
Apr spring	62.9	896	133.6± 48.53(17)	75.29	2.95	(3.59/25%)
May spring	55.9	1003	350.2±104.16(33)	196.35	7.70	(8.07/5.3%)

Notes

[1]Each estimate of PFT is based on the equivalent of at least one full tidal cycle, usually more (see text).

[2]To help estimate possible variation, the effect of adding one *Arenicola* to those observed in each weather condition/month on the intake is indicated (see text); given as (factor x BMR/ % theoretical increase in *Arenicola* taken).

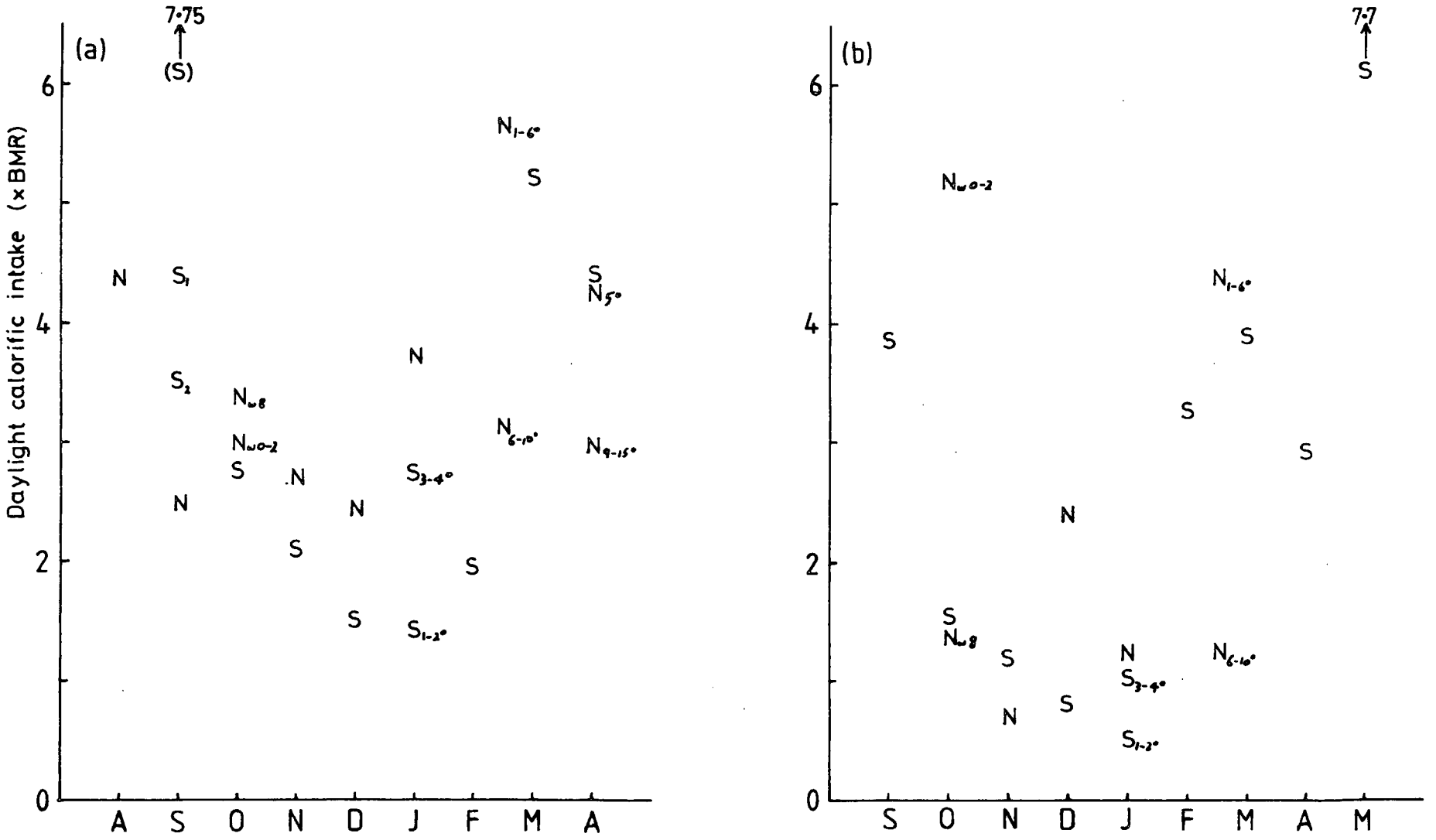


Figure 9. Seasonal variations in daylight calorific intakes, expressed as the number of BMR equivalents for (a) Ringed Plover and (b) Grey Plover. S = spring tides; N = neap tides; (S) = juveniles. Separate estimates for different wind forces (w) or temperatures (^{o}C) indicated where available.

PFT, e.g. for Ringed Plover PFT was depressed by about 8% by the squalls on 24 January 1976. Unless feeding was inhibited by such extremely adverse conditions, increased PFT's usually occurred with low temperatures and high winds (Fig. 8).

PFT's, daylight duration and mean intake rates are combined in Tables 14 & 15 to estimate average daytime calorific intakes. These are compared with Basal Metabolic Rates (BMR) of 10.45 kcal/day and 25.5 kcal/day for Ringed and Grey Plovers respectively, estimated from Lasiewski & Dawson's (1967) equation for non-passerines and based on mean lean weights of 62 g and 212 g (N.C. Davidson pers. comm.). The seasonal relationship between estimated daytime intake and BMR is plotted in Fig. 9.

DISCUSSION

Diet

In the main study area of Holy Island Sands, the polychaetes *Arenicola*, *Notomastus* and *Scoloplos* clearly provided the main prey in terms of both numbers and energy content for the two plover species in daylight. There is reason to believe that *Phyllodoce* may have been a numerically important prey at night (Paper 2). Additional prey species included bivalves (*Macoma*, *Cerastoderma*), gastropods (*Hydrobia*, *Littorina*, *Gibbula*) and Crustacea (*Carcinus*, *Bathyporeia*, *Eurydice*). Generally, of the two plovers, the larger Greys tended to take larger items (both more larger species and more large individuals of a given species) than the smaller Ringed Plovers, and the small amphipods and isopods taken mainly at high tidal levels were probably important only to the latter birds.

When feeding on Fenham Flats, Grey Plovers took mainly *Nereis*, probably supplemented by *Hydrobia* and *Macoma*. Great flexibility in both principal and less important prey is evident when studies from other areas are also taken into account (Tables 16 & 17). Not only does the prey of individual species tend to vary greatly but within a particular coastal area different bird species often take similar species of prey (Table 16), these normally being among the most abundant invertebrate species present.

TABLE 16. MAIN PREY TAKEN BY VARIOUS SPECIES OF WADERS, MAINLY AT SITES WHERE A RANGE OF SPECIES HAVE BEEN STUDIED

	LEDSKAR[1]	HUSUM[2]	HOHWACHT[2]	HELGOLAND[2]	ESSEX[3]	TEESMOUTH[4]	LINDISFARNE[5]	THE WASH[6]	SWARTKOPS[7] S. AFRICA
CHARADRIIDAE									
Ringed Plover	Coleoptera	*Nereis*	Coleoptera Diptera	*Littorina*	-	*Nereis* *?Corophium*	*Notomastus* *Scoloplos* small crustacea *Arenicola*	-	-
Grey Plover	-	*Nereis*	-	-	*Hydrobia*	*Nereis* *Hydrobia*	*Arenicola* *Notomastus* *Scoloplos* *Nereis*	*Lanice* other polychaetes *Macoma* *Cerastoderma* *Hydrobia*	*Upogebia* (mud prawn) *Cleistosoma* (small crab) Other crabs *Assiminea* (small gastropod)
SCOLOPACIDAE									
Curlew	-	*Nereis*	-	-	*Carcinus*	*Nereis*	-	*Lanice* *Arenicola* *Carcinus* other polychaetes & bivalve molluscs	
Bar-tailed Godwit	-	*Nereis*	-	-	-	*Nereis*	*Arenicola* *Notomastus* *Scoloplos* *Nereis*	*Lanice* *Nereis* *Macoma* other polychaetes & bivalve molluscs	
Redshank	Coleoptera	*Nereis*	-	-	*Hydrobia*	*Nereis* *Hydrobia* *Macoma*	-	*Hydrobia* *Macoma* *Carcinus* *Nereis* *Crangon* amphipods	
Knot	-	*Hydrobia* *Littorina*	-	-	-	*Mytilus* *Hydrobia* *Macoma*	-	*Macoma* *Cerastoderma* *Hydrobia* *Mytilus*	
Dunlin	Coleoptera	*Nereis*	Diptera	-	*Hydrobia*	small oligochaetes & polychaetes *Nereis* *Hydrobia*	small oligochaetes & polychaetes *Notomastus* *Scoloplos* *Hydrobia* small crustacea	*Hydrobia* *Nereis* small worms	

SOURCES: [1]Norlin (1965) in autumn; [2]Hofmann & Hoerschelmann (1969), mainly in autumn; [3]Burton (1968, 1974 & *in litt.*) mainly in winter; [4]Pienkowski (1973), Evans *et al.* (1979) in autumn and winter; [5]Evans & Smith (1975), Smith (1975), Pienkowski (this study) in autumn and winter; [6]Pienkowski (1972), Goss-Custard, Jones & Newbery (1977) in autumn & winter; [7]Schramm (1978) throughout the year.

TABLE 17. IMPORTANT PREY OF SOME WADERS AS RECORDED BY VARIOUS STUDIES

		Mollusca							Crustacea							Annelida							Insecta	Pisces
		Mytilus	*Mya*	*Cerastoderma*	*Macoma*	*Scrobicularia*	*Hydrobia*	*Littorina*	*Carcinus* & other crabs	*Crangon*	*Talitrus*	*Corophium*	*Artemia*	Small Amphipoda & Isopoda	Mysidacea	*Lanice*	*Arenicola*	*Notomastus*	*Scoloplos*	*Nereis*	Small Polychaeta & Oligochaeta	Larvae	Adults	
Charadriidae	Oystercatcher *Haematopus ostralegus*	*	*	*	*			*	*											*				
	Ringed Plover *Charadrius hiaticula*				*		*	*			*	*		*	*		*	*	*	*	*	*	*	
	Kentish Plover *C. alexandrinus*						*	*	*						*					*		*	*	
	Grey Plover *Pluvialis squatarola*	*	*	*	*		*	*	*	*						*	*	*	*	*				
Scolopacidae	Curlew *Numenius arquata*			*	*	*	*		*							*	*			*			*	
	Bar-tailed Godwit *Limosa lapponica*			*	*		*									*	*	*	*	*	*	*		
	Redshank *Tringa totanus*	*		*	*		*	*	*	*		*		*						*	*	*	*	*
	Knot *Calidris canutus*	*		*	*		*	*	*			*								*	*	*	*	
	Little Stint *C. minuta*						*						*	*							*	*	*	
	Dunlin *C. alpina*	*		*	*		*	*	*			*	*	*	*			*	*	*	*	*	*	
	Curlew Sandpiper *C. ferruginea*				*		*							*						*		*	*	

Sources: Those given for Table 16 plus: Baker (1974), Bengtson & Svensson (1968), Dare & Mercer (1973), Davidson (1971), Ehlert (1964), Evans (1974, 1975), Fuchs (1975), Goss-Custard (1969), Heppleston (1971), Moran & Fishelson (1971), Prater (1972), Smyth (1954), Thomas & Dartnall (1971) & Viellard (1973).

Goss-Custard (1977a) has argued that some shore-bird species may have favoured prey, these being taken in preference even to other items which provide a higher energy return per unit time when a choice of prey is present. Despite this, most shorebirds are clearly not restricted to such preferred prey and are able to utilize different species in different situations, as suggested also by Smith (1975). Rather than being adapted to take particular types of prey, it seems more likely that waders have specialized in the way they exploit the behaviour of prey (Pienkowski 1980) and this is explored further in Paper 2. Oystercatchers may represent a partial exception as Norton-Griffiths (1967) has shown them to specialize in taking particular prey species and, in some cases, in the way these are taken. This is, however, an exceptional wader species in that the adults feed their young, thus allowing maintenance of specialized feeding habits from generation to generation.

Feeding areas

Several workers have demonstrated that waders tend to feed in the areas of highest densities of the predominant prey species being taken in that area (e.g. Goss-Custard 1970a, 1977b, Goss-Custard, Jones & Newbury 1977, Goss-Custard, Kay & Blindell 1977, O'Connor & Brown 1977, Smith 1975, Wolff 1969, Zwarts 1974). Comparison of the low-water distribution patterns of the two plover species with their main prey (Figs. 2, 3) suggests this is true at Lindisfarne also, both species using the densest areas of 'red worms' on east HIS and west of Old Law, and the Grey Plovers also spreading out over Fenham Flats where *Nereis* was abundant (although difficulty of access on the soft mud of this area prevented systematic sampling). Lack of time and access difficulties also prevented detailed study of the foraging of plovers on Fenham Flats.

As the tide rose the movements of the plovers differed somewhat, the Greys tending to move north-westwards over HIS, eventually roosting over high-water on either the Snook saltmarsh (neaps) or the Sand Rig (springs). The Ringed Plovers tended to move rapidly north, once the rising tide had passed the 'Pilgrims' Way' at 'Ringed Plover Gully', to within about 100 m of the road or in some instances to the North Shore of the Snook where feeding continued over high water on neaps

or until the area was covered on spring tides. The difference between the species is probably also related to invertebrate distribution, for at higher tidal levels Ringed Plovers fed on small Crustacea which occur most abundantly (although very variably in position along shore after each tide) along the north and south shores of the Snook (Figs. 2, 3). As the tide rose Grey Plovers tended to continue feeding on *Arenicola*, other worms and probably various small molluscs which occur in highest densities away from the northern and eastern limits of HIS (Figs. 2, 3). Ringed and Kentish Plovers *C. alexandrinus* also concentrated on the areas of the highest density of small Crustacea (in this case Mysids) on the shore in Israel (Moran & Fishelson 1971).

In order to obtain a more quantitative assessment of the relationship between plover distribution and prey density, the presence or absence of feeding Ringed Plovers was recorded during the low water period on 18 occasions in early winter in 12 adjoining squares of 100 m sides across the high density area of red worms on eastern HIS (Table 18). Plovers were not recorded in the squares of lower prey density but on almost half the occasions in those of high prey density. Clearly the plovers were tending to use the areas of highest density of the main prey but other factors were also strongly involved. These probably include the presence of other birds and the behaviour and availability of the potential prey (Pienkowski 1980). Such factors will be explored further in Paper 2.

Impact of birds on their prey

The impact of large concentrations of shore birds on the numbers of their prey is of interest in terms of the population dynamics of the prey and the implications for the shorebirds, especially in terms of possible loss of feeding areas as a result of current large scale land reclamations. An unsuccessful attempt was made to use an exclosure experiment to measure this impact on the worms which formed, numerically, the most important component of the plovers' diet. Millard (1976) and Millard & Evans (unpublished MS) have reviewed the problems with this method resulting from movements of sediment and prey in an intertidal situation. Their work was concerned chiefly with the amphipod *Corophium volutator* and the gastropod *Hydrobia ulvae* both of which live very close to - or, for some *Hydrobia*, on - the

TABLE 18. DISTRIBUTION OF RINGED PLOVERS AT LOW WATER IN SQUARES WITH SIDES OF 100 M, IN RELATION TO PREY DENSITIES IN THESE SQUARES

		Densities of thin red worms		
		<1500/m^2	>1500/m^2	TOTAL
RINGED PLOVERS	PRESENT	0	48	48
	ABSENT	108	60	168
TOTAL		108	108	216

$\chi^2_1 = 61.72$ $P << 0.001$

surface of the mud. Basing their comments on the observations of Vader (1964) on *Scoloplos armiger* and Brafield & Newell (1961) on *Macoma balthica*, Millard & Evans predicted that these species would also be too mobile for exclosure experiments to be practicable. The present work has confirmed this for these and for *Notomastus*.

An alternative method of assessing the impact of the birds on their invertebrate prey was based on measuring feeding rates, counting the feeding birds present in two 100 m x 100 m study areas throughout the daylight tidal cycle and comparing the numbers of worms taken with the change in density of worms estimated by sampling on three occasions (Table 19).

Notomastus showed a marked and significant decrease in density in both sites between November and February and slight but non-significant further decreases by May. Because of the lack of studies on *Notomastus*, it is not known whether losses during reproduction could have been involved in these changes. Changes in density of *Scoloplos* and *Macoma* were generally non-significant, although there were slight signs of decrease in the former. Significant differences between stations on the sampling grid were evident in the *Notomastus* samples, implying that the fixed-station, paired-samples method may be an improvement over random sampling here for investigating seasonal changes. No such significant effect was found for *Scoloplos* and *Macoma*, possibly implying greater mobility in these species during the periods between sampling.

Despite the number of factors involved in their calculation, the large variances (leading to lack of significance of the invertebrate density changes), and the lack of information on the life-cycle of *Notomastus*, the estimates for prey removed and density reductions between February and May show remarkably good agreement in both sites. Estimates of numbers taken are somewhat lower than those given by mud-sampling, but this is not surprising, as the number of worms taken by Dunlins could not be estimated accurately. This is because Dunlins tend to swallow some prey without removing the bill from the substrate. However, it is mainly small prey rather than long worms which are dealt with in this way, suggesting that relatively few large worms are

TABLE 19. COMPARISON OF NUMBERS OF RED WORMS TAKEN BY WADERS WITH CHANGES IN DENSITY OF RED WORMS OVER THE SAME PERIODS

	Feeding bird-min /daylight tide	Thin red worms taken/min			Total no. of thin worms taken over period in daylight tides by plovers and godwits		
		minimum	estimate	maximum	minimum	estimate	maximum
20 Nov 1974 to 20 Feb 1975 (92 days)							
Area B							
Ringed Plover	2055	3.15	7.48	11.53	595,539	1,414,169	2,179,862
Grey Plover	999	2.16	4.21	6.12	198,521	386,933	562,477
Bar-tailed Godwit	1443		1.5		199,134	199,134	199,134
Dunlin	10548		?		?	?	?
				Total	993,194	2,000,236	2,941,473
Decrease in no. of red worms in period = 6,944,000 *Notomastus* + 2,806,000 *Scoloplos* = 9,750,000							
Area D							
Ringed Plover	973	3.15	7.48	11.53	281,975	669,580	1,032,119
Grey Plover	317	2.16	4.21	6.12	62,994	122,780	178,484
Bar-tailed Godwit	23		1.5		3,174	3,174	3,174
Dunlin	3980		?		?	?	?
				Total	348,143	795,534	1,213,777
Decrease in no. of red worms in period = 6,131,000 *Notomastus* + 305,000 *Scoloplos* = 6,436,000							
20 Feb to 23 May 1975 (92 days)							
Area B							
Ringed Plover	42	4.45	11.09	16.71	17,195	42,852	65,467
Grey Plover	1188	2.51	4.67	6.67	274,333	510,412	729,004
Bar-tailed Godwit	879		1.5		121,302	121,302	121,302
Dunlin	5238		?		?	?	?
				Total	412,830	674,566	914,873
Decrease in no. of red worms in period = 1,528,000 *Notomastus* (-473,000 *Scoloplos* = 1,055,000)							
Area D							
Ringed Plover	627	4.45	11.09	16.71	256,694	639,716	963,900
Grey Plover	317	2.51	4.67	6.67	73,201	136,196	194,524
Bar-tailed Godwit	0		-		0	0	0
Dunlin	3082		?		?	?	?
				Total	329,895	775,912	1,158,424
Decrease in no. of red worms in period = 435,000 *Notomastus* + 608,000 *Scoloplos* = 1,043,000							

taken here. In some areas Dunlins are known to take large quantities of meiofauna, Evans *et al.* (1979) having shown that small annelids form most of the intake of this species at Teesmouth. Worms of this type are also abundant in the study area of HIS and elsewhere at Lindisfarne, particularly on Fenham Flats.

In the earlier period of the winter the estimated numbers taken were far less than those calculated from the changes in density. It is at this time of year that night feeding is common but, as feeding rates were less at night than during the daytime and numbers of birds feeding at night did not appear to exceed those during the day, possibly the numbers of prey taken at night did not exceed those taken during daytime, even though nights are long at this time of year. Comparisons of intake in mid-winter with that in autumn and spring (Tables 14 & 15, Fig. 10) suggest, however, that in mid-winter Ringed Plovers might be expected to take as many prey items during the night as in daytime and Grey Plovers twice the daytime intake. If the estimated numbers of worms taken are increased in these proportions, losses due to birds in area B approaches half the decrease measured by density changes and in area D about one-third. Thus much of the decrease in density between November and February is likely to be due to other causes. These are unknown but could include predation by other animals such as fishes and downshore migration of worms, as is known to occur in *Arenicola marina* (Green 1968, Darby 1975, Smith 1975). Unfortunately, no comparable study of *Notomastus* appears to have been made.

If the greater percentage fall in *Notomastus* density in area D (with lower initial density) than area B was due to predation, this appears to run counter to suggestions that birds "graze" down the invertebrates from high density areas first (see Goss-Custard 1970a, Heppleston 1971, Prater 1972, Smith & Dawkins 1971, Smith & Sweatman 1974, O'Connor & Brown 1977). Possibly the higher predation in D, if real, results from greater densities of available worms in this wetter area where they tend to be nearer the surface (Paper 2).

Considerable differences in the extent of changes in density of intertidal invertebrates between autumn and the following spring have

been reported, e.g. a 50% reduction in *Macoma* on Morecambe Bay (Anderson 1972) and a 90% reduction in *Hydrobia* and 80% in *Nereis* at Teesmouth (Evans *et al.* 1979). In other areas reductions have been as little as 14% (*Macoma* & *Cerastoderma* in one study area at the Wash - Goss-Custard 1977b). The estimated overwinter impact of shore-birds has also differed greatly in different situations: birds were estimated to consume 42-84% of the benthic production of the Waddenzee (Hulscher 1975); Bar-tailed Godwit 26% of the standing crop of *Arenicola* on HIS (Smith 1975); Knot 24%, 34% and 2% of the standing crop of *Macoma* and *Cerastoderma* at 3 sites on the Wash and Oystercatchers 21%, 12% and 14% of the standing crop of *Cerastoderma* at the same sites (Goss-Custard 1977b); shorebirds removed 90% of the standing crop of *Hydrobia* and 93% of *Nereis* at Teesmouth (Evans *et al.* 1979). In a terrestrial situation in Iceland in spring, Golden Plovers *Pluvialis apricaria* reduced the population of lumbricid earthworms by about 50% (Bengtson *et al.* 1976). At HIS, the November to May reduction in density in the two sites of *Notomastus* was 38% and 97% and of *Scoloplos* 18% and 34%, but losses of only 8% and 17% of the initial numbers of these worms in the two areas could be attributed to predation by plovers and Godwits in daytime, although it is possible that Dunlins took a further amount. The losses calculated here relate to numbers of worms estimated from observed feeding rates and numbers of birds feeding in the areas in daylight, in contrast to the values from other studies cited (except Smith 1975) which depend on estimates of the energy requirements of the birds and calorific values of the prey. Energetic considerations discussed in the following section suggest that, in mid-winter, Ringed Plovers must intake about the same amount of energy by night as by day and Grey Plovers about twice as much by night as by day. Smith's (1975) work suggests that nocturnal intake by Bar-tailed Godwits is small. If one assumes similar feeding distribution by night and by day and multiplies the numbers of worms taken in daylight in November to February by the two plover species by 2 and 3 respectively while leaving the godwit impact and that of the plovers in February to May as before, the losses due to birds can be increased from 8% and 17% to 14% and 26%.

We do not know to what level prey densities must be reduced before feeding rate or efficiency is reduced, even without the complication of varying prey availability, although this is considered tentatively

in Paper 2. Further, there is no reason to suppose that initial prey density is related to this in any way, so that the value of comparisons of percentage reductions in prey density is dubious. The absolute numbers of prey taken in an area may, however, have relevance to further hunting there if this can be assessed by the bird, according to the system put forward by O'Connor & Brown (1977) in which Oystercatchers may avoid areas where opened cockle *Cerastoderma edule* shells are already abundant.

The reduction in prey density at HIS did not appear to affect feeding rates of the plovers (Tables 14 & 15) which increased slightly in the period after February as might be expected at higher temperatures (Pienkowski 1980; see also Paper 2). Plovers appear to be able to forage effectively at low prey densities (Pienkowski 1980), and large reductions in prey density over winter must be faced by many waders (see above). Equally the impact of the birds on the worms appears to be small compared with other studies. It seems unlikely that low prey density imposes constraints on plovers at Lindisfarne, although availability of prey may be important and this will be considered further in Paper 2.

Energy balance

In many shorebirds, including the plovers, potential feeding time in daylight appears to be in short supply in mid-winter. Therefore it seems reasonable to suppose that waders may be adapted to maximise their net rate of energy input (i.e. energy from food assimilated less the energetic cost of foraging) per unit time. In addition, minimizing the time spent feeding may allow increased alertness against predators, as indeed would flocking. Predation is clearly an important influence in some situations (Page & Whitacre 1975, Smith 1975) and shorebird behaviour appears to be adapted to avoid this (Goss-Custard 1970b, Smith 1975, Owen & Goss-Custard 1976). In many situations the maximizing of biomass intake per unit time may be equivalent to maximizing the rate of net energy gain (which is itself not normally directly measurable) and Goss-Custard (1977c) has presented evidence that the former is maximized in Redshank in at least some circumstances. However, as pointed out by Evans (1976), the costs per unit time of foraging relative to the rate of net energy gain may differ in different

circumstances so that a method maximising biomass intake per unit time may not always be the method leading to the shortest feeding time, particularly if this method is costly in energetic terms.

Several studies have indicated that sandpipers and Oystercatchers meet their energy requirements by feeding in daylight if they can (Goss-Custard 1969, Heppleston 1971, Pienkowski 1973, Smith 1975, Evans 1976, Goss-Custard *et al.* in prep.) One would expect this tendency to be even greater in plovers which forage by an apparently visual, rather than tactile, technique (see also Paper 2). Pecking rate is, indeed, generally depressed at night (Table 10) as was also found for Grey Plovers feeding on *Nereis* at Teesmouth (Evans 1976). As in daytime at least 90% of pecks result in a prey item being taken, this must mean that the rate of taking prey is depressed at night. It is also likely that rate of energy intake is lower at night than by day, as no *Arenicola* were seen to be taken at night although some small worms were. Considerations of invertebrate behaviour (see Paper 2) suggest that these thin worms included *Phyllodoce*, a worm of approximately similar size to *Notomastus*. Smith (1975), watching Bar-tailed Godwits feeding at night on HIS, also saw no *Arenicola* in the prey taken in an area where *Arenicola* were taken by day, although other worms were seen. Hulscher (1974, 1976) found little or no decrease in rate of energy intake at night compared with that during the day for captive Oystercatchers which could use tactile foraging at night, although Drinnan (1958) and Heppleston (1971) both found reductions for the same species.

It is possible that other prey in different areas are more available at night. The nocturnal emergence of earthworms may be the reason for the nocturnal activity of field-feeding Golden Plovers *Pluvialis apricaria* and Lapwings *Vanellus vanellus*. At the Ythan estuary, Scotland, Goss-Custard (1969) noted a change in feeding area used by Redshanks between day and night. There was no evidence of any movement by the shore plovers at Lindisfarne to fields at night and such behaviour has not been noted by the local residents many of whom are very active wildfowlers and extremely knowledgeable about the nocturnal movements of the shorebirds. It is also possible that the Grey Plovers make more use of Fenham Flats at night. If this were the

case, however, it is surprising that the birds should increase their nocturnal use of HIS in mid-winter, when their nocturnal food requirements are highest, rather than continue to use Fenham Flats. (However, this might result if the effects of low temperatures on the nocturnal activities of different prey species differed markedly.) Some degree of feeding at night by plovers on HIS was evident from October to March, particularly in November to February, the times when energy intake in daylight was lowest (Fig. 9).

Interpretation of Figure 9 requires some care as it is built up of various parameters (Tables 14, 15) each of which may have a considerable error attached to it. Because of the large quantity of data required to calculate PFT for a given set of conditions, no standard error can be attached to each estimate but some indication of the variation is given by the two estimates of PFT available for September spring tide conditions, used to give the points S1 and S2 in Figures 8 & 9. Despite these problems the fairly consistent seasonal pattern in Figure 9 gives some support to the estimates.

Some of the standard errors of mean feeding rates in Tables 14 & 15 are large, particularly those for Grey Plovers and some for Ringed Plovers in autumn and spring. This was not due to any consistent hour-to-hour or day-to-day variation but arose because the rate of taking *Arenicola* was low and this prey occurred in a few observation cases and not in most. In order to give some indication of the scale of the effect of *Arenicola* on intake rates, Table 14 & 15 also include in parentheses an additional column of daytime intake as a multiplier of BMR. This was obtained using a value for calorific intake per minute which assumed that, had one more peck in each weather condition/month been watched, this peck would have produced an *Arenicola*. Also given in the parentheses are the percentage increases in numbers of *Arenicola* taken which this theoretical addition involves. It is unlikely that a systematic error of this nature could have arisen. This is especially so for Ringed Plovers which did not take *Arenicola* at all in most conditions; this is why intake rates for Ringed Plovers were less variable than for Greys. However, some error in estimation of the number of *Arenicola* taken could account for the very low values of daytime intake rate calculated for Grey Plovers in mid-winter (see

below).

The increase in PFT in winter is clearly insufficient to compensate for the decreases in both daylength and feeding rate which occur at this time. The situation for Ringed Plovers appears to be more critical during spring tides than neaps because feeding areas may be unavailable for up to 30% of the time, over high water of spring tides. In some species which feed at the tide edge the additional exposure at low water of spring tides of rich prey areas appears to compensate for loss of feeding time over high water e.g. utilization of mussel beds by Knots on Morecambe Bay (Prater 1972) and feeding on *Lanice* by Bar-tailed Godwit and Curlew at Lindisfarne and the Wash (Smith 1975, Evans 1976, Goss-Custard, Jones & Newbery 1977). In Ringed Plovers this does not appear to be the case as the birds do not change their feeding area and prey between spring and neap tides. The pattern is less clear in Grey Plovers, possibly because sample sizes for both feeding rates and PFT estimates were generally smaller and variation higher due to the more dispersed feeding distribution of these larger birds, as well as the effect of the low rate of capture of *Arenicola*, discussed above.

What are the energy requirements of these birds? Ebbinge, Canters & Drent (1975) reviewed published data which showed that a variety of wild birds require energy to be assimilated at a rate of between 2 and 4 x BMR in order to maintain body temperature, move about and feed. Evans *et al.* (1979) considered that, because of their energy-demanding methods of foraging, the upper figure is most appropriate for sandpipers and, because of the 80%-90% assimilation of ingested food, 4.5 x BMR is an appropriate factor for estimation of food intake. Because of the apparently less active method of feeding 3.5 x BMR was considered suitable for Grey Plovers. Field studies of waders have given values summarised in Table 20.

It should be noted that no direct measures of BMR for these plovers is available and the following discussion assumes that the general relationship calculated by Lasiewski & Dawson (1967) applies to these birds. If it does not, the conclusions may require amendment.

TABLE 20. PUBLISHED VALUES OF DAILY ENERGY INTAKE AS A MULTIPLIER OF BASAL METABOLIC RATE ESTIMATED IN FEEDING STUDIES OF WADERS

Species	Situation	Daily intake (x BMR)	Source
Oystercatcher	captivity	4.3	Hulscher (1974)
"	field	6.8	Smith (1975), using data from Davidson (1968) & Hulscher (1974)
"	"	5.8	Goss-Custard (1977b)
Bar-tailed Godwit	captivity	3	Smith (1975)
"	field	5	" "
Redshank	field	4.2 to 5.0	Goss-Custard (1977b)

In August, September and April at Lindisfarne there was almost no night feeding of plovers and feeding intensities in daytime were frequently below 100%. Also the winter difference between neap and spring daylight intakes in Ringed Plovers disappeared. This suggests that daylight estimates for these months are reasonable ones for total intake. August and September estimates for Ringed Plovers are 2.5, 3.5, 4.4 and 4.4 x BMR and for Grey Plovers 3.9 x BMR. In April, values were 3.0, 4.3 and 4.4 x BMR for Ringed Plovers and 3.0 for Grey Plovers. Values in August and September may be slightly higher than survival requirements because birds are involved in their full annual moult at this time. In April Grey Plovers and possibly Ringed Plovers may also be involved in moult of the contour feathers. Metabolic rate in a variety of mainly passerine species during moult increased by between 5 and 30% over that of non-moulting birds (Payne 1972). However, during moult most song birds tend to be less active than at other times (e.g. Haukioja 1971, Payne 1972, Green & Summers 1975) and this appears to apply also to waders despite their potential vulnerability and need to move in relation to the tide in open, coastal habitats (e.g. Pienkowski & Dick 1976), so that there may be a compensatory reduction in energetic requirements for activity. Payne (1972) considered that the energy requirements for moult were small compared with those concerned with thermoregulation, migration and breeding. It seems, therefore that 3.5 x BMR is a reasonable value for plovers.

This value was greatly exceeded in two situations. In September juvenile Ringed Plovers which were probably still growing fed at a rate equivalent to 7.8 x BMR. In May the intake of Grey Plovers which were probably depositing pre-migratory fat was equivalent to 7.7 x BMR.

During winter, intakes during daylight fell to about 2 x BMR for Ringed Plovers and about 1 x BMR for Grey Plovers despite generally higher PFT's of the latter. Earlier studies at Teesmouth (Pienkowski 1973, 1979) and the Wash (Goss-Custard *et al.* 1977) found that within birds of similar feeding behaviour, smaller birds generally fed for longer times than larger ones, the result of high metabolic rates per unit weight in small birds, this in turn arising from both the greater rate of heat loss due to large surface area and the thinner

plumage of small birds (Kendeigh 1970). However, if the birds are taking substantially the same size of prey - and at Lindisfarne there seems to be considerable overlap in the diet of the two plover species - this may not hold because of the higher absolute requirements of the larger birds. Smith (1975) noted that Bar-tailed Godwits at Lindisfarne feeding on *Arenicola* fed for a shorter time each day than those at Teesmouth feeding on smaller *Nereis* (observed by P.J. Knights).

For any given month the daylight intake of both plover species at Lindisfarne showed a considerable range in values. While this is clearly due in part to the difficulties in estimation, large day-to-day fluctuations were also observed by Hulscher (1974) in captive Oystercatchers for which measures were more readily obtained. Further, large fluctuations might be expected in birds which could not balance their intake and requirements on some days but compensated on others, a situation which seems possible in the plovers. As the data on intake rates and feeding times had to be pooled form several days, day-to-day variation and slight changes with environmental conditions could not be assessed in detail, but must have been even greater than the "composite" values used in these calculations.

The daytime intake of plovers appears to fall much more in mid-winter than do those of sandpipers. For example, in December Bar-tailed Godwits at Lindisfarne maintained intakes equivalent to 2.9 to 5.1 x BMR (Smith 1975). With daytime intakes of only about 1 x BMR it is likely that many Grey Plovers must be near minimum levels for survival even if feeding is maintained throughout the night. It is not surprising that plovers tend to winter further south than do sandpipers (Pienkowski 1980). As waders deposit fat (and possibly protein) as an "insurance" against short-term negative energy balances (Evans & Smith 1975, Evans 1976, Pienkowski, Lloyd & Minton 1979), higher reserves in plovers than sandpipers might be expected and they are indeed heavier (Eades & Okill 1976, Clapham 1978, Pienkowski 1980, N.C. Davidson pers. comm). Those Ringed, Grey and other plovers wintering in warmer areas, in common with other waders, do not show overwinter weight increases (Dick & Pienkowski 1979, Summers & Waltner 1979). The peak mid-winter weights of plovers probably indicate fat reserves which would allow survival for about a week. If the reserves are used for 'topping-up' inadequate

feeding rather than as a sole energy source they could probably last much longer, allowing survival over quite long periods of adverse weather. However, strong winds, especially at night, appear to deter many birds from feeding at all and during such periods the reserves must supply all energy requirements.

Plovers at Lindisfarne also appear to suffer a decrease in energetic intake earlier in the autumn than sandpipers - Bar-tailed Godwits in October at Lindisfarne had intake rates equivalent to 5.2 to 5.6 x BMR. This may be the reason why fat reserves (as indicated by body weights) appear to be built up by plovers to a high level earlier in autumn than many other species of waders (Minton 1975, Clapham 1978). This aspect of plovers has long been known to wildfowlers and Bolam (1912), in describing Grey Plovers in the Lindisfarne area, noted "like most of their kindred, they are seldom otherwise than in excellent condition, and are, as a rule, quite as good as Peewits on the table." The fall in intake early in the season may also relate to the primary moult pattern of Grey Plovers at the Waddenzee (Boere 1976) and the Wash (Branson & Minton 1976). Alone among waders studied in these areas, many individuals (about 16%) of this species commonly arrest moult in November with one to five old primaries remaining, these normally being replaced the following spring starting in mid-March but in a few cases being retained to the following autumn. Possibly the arresting of moult is an adaptation to low intake rates. This arresting did not appear to occur in Mauritania (Dick 1976), and in general the more favourable condition in the non-breeding season at southern latitudes allow prolonged moult during this period (Pienkowski *et al.* 1976).

Why does the energy intake of plovers fall so steeply from autumn to winter? Plovers are subject to the same daylight period as other species and appear able to maintain PFT's as high and often higher than those of sandpipers, probably because of their ability to feed at high tidal levels on low prey density. The difference lies in the greater depression of intake rates per unit time of plovers. Some reasons for this have already been mentioned, but they are explored in detail in Paper 2.

SUMMARY

The diets, feeding rates, foraging times during daylight, the extent of nocturnal feeding and food intakes of Grey and Ringed Plovers are described or estimated from field observations at Lindisfarne, Northumberland, in the years 1973-76. Ciné-film was used to check the validity and reliability of direct observations. Gut analysis was unreliable as a quantitative guide to diet. Main prey at Lindisfarne for both plovers were the polychaete worms *Notomastus*, *Arenicola* and probably *Scoloplos* and *Phyllodoce* and, for Ringed Plovers, also various small Crustacea, particularly *Bathyporeia* and *Eurydice*.

Densities of the prey were sampled on three occasions during the 1974-75 winter and attempts made to assess the impact of the birds on their prey. Although both plovers tended to feed in the areas of highest density of their prey, comparisons with diets of the same species reported from elsewhere showed that they are not specialized but vary their diet in accordance with the prey species common in a particular area.

In autumn and spring, food requirements could be met during daylight but this was not possible in winter. Although they increased the percentage of the daylight hours spent feeding in winter, this was inadequate to compensate for the decreases in both hours of daylight and feeding rate which occur at this season, especially during spring tides when potential feeding time is reduced, since their feeding grounds may be covered for half the daylight hours on some days. Both plovers were able to feed at night but, on dark nights at least, at a slower rate than by day. The birds apparently fed at night only when food requirements could not be met by daylight feeding. High winds apparently depressed the extent of nocturnal feeding. In mid-winter, the birds maintain high fat levels, probably to buffer the effects of days when they have difficulty in obtaining their energy requirements, such as during cold and windy weather.

Because plovers' feeding rates are reduced more by low temperatures than those of waders foraging by touch, their rates of energy intake fall more in such conditions.

REFERENCES

Anderson, S.S. 1972. The ecology of Morecambe Bay. II. Studies on the intertidal invertebrates of Morecambe Bay and factors affecting their distribution. *J.appl.Ecol.* 9: 161-178

Bailey, N.T.J. 1959. *Statistical Methods in Biology*. English Univ. Press, London

Baker, M.C. 1974. Foraging behaviour of Black-bellied Plovers (*Pluvialis squatarola*). *Ecology* 55: 162-167

Bengtson, S.-A., Nilsson,A., Nordström, S. & Rundgren, S. 1976. Effect of bird predation on lumbricid populations. *Oikos* 27: 9-12

Bengtson, S.-A., & Svensson, B. 1968. Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. *Oikos* 19: 152-157

Boere, G.C. 1976. The significance of the Dutch Waddenzee in the annual life cycle of arctic, subarctic and boreal waders. Part 1. The function as a moulting area. *Ardea* 64: 210-291

Bolam, G. 1912. *Birds of Northumberland and the Eastern Borders*. 2nd ed. Henry Hunter Blair, Alnwick

Brafield, A.E. & Newell, G.E. 1961. The behaviour of *Macoma balthica*. *J.mar.biol.Ass. U.K.* 41: 81-87

Branson, N.J.B.A. & Minton, C.D.T. 1976. Moult, measurements and migrations of the Grey Plover. *Bird Study* 23: 257-266

Burton, P.J.K. 1966. Food and feeding methods of Curlew, Golden Plover and Lapwing. *Ibis* 108: 455

Burton, P.J.K. 1974. *Feeding and the feeding apparatus in waders*. British Museum (Natural History), London

Clapham, C. 1978. The Ringed Plover populations of Morecambe Bay. *Bird Study* 25: 175-180

Darby, J. 1975. Dispersion patterns of the lugworm *Arenicola marina*. Unpublished Hons. Thesis, Department of Zoology, University of Edinburgh

Dare, P.J. & Mercer, A.J. 1973. Foods of the Oystercatcher in Morecambe Bay, Lancashire. *Bird Study* 20: 173-184

Davidson, P.E. 1967. A study of the Oystercatcher (*Haematopus ostralegus* L.) in relation to the fishery for Cockles (*Cardium edule* L.) in the Burry Inlet, South Wales. *Fishery Invest.,Lond.* (Ser. II) 25(7): 1-28

Davidson, P.E. 1968. The Oystercatcher - a pest of shell-fisheries. Pp 141-155 in R.K. Murton & E.N. Wright (Eds.) *The Problems of Birds as Pests*. Academic Press, London

Davidson, P.E. 1971. Some foods taken by waders in Morecambe Bay, Lancashire. *Bird Study* 18: 177-186

Dick, W.J.A. (Ed.) *Oxford & Cambridge Mauritanian Expedition 1973 Report.* Cambridge

Dick, W.J.A. & Pienkowski, M.W. 1979. Autumn and early winter weights of waders in north-west Africa. *Ornis Scand.* 10: 117-123

Drinnan, R.E. 1958. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the Edible Mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. *Fishery Invest.,Lond.* (Ser. II) 22(4): 1-15

Eades, R.A. & Okill, J.D. 1976. Weight variations of Ringed Plovers on the Dee Estuary. *Ringing & Migration* 1: 92-97

Ebbinge, B., Canters, K. & Drent, R. 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. *Wildfowl* 26: 5-19

Ehlert, W. 1964. Zur Okologie und Biologie der Ernshrung einiger Limikolen-Arten. *J.Orn.* 105: 1-53

Evans, P.R. 1974. Exploratory investigation of feeding ecology and behaviour of shorebirds in Westernport Bay. Report on project W38/74 Westernport Bay Environmental Study, Victoria, Australia

Evans, P.R. 1975. Notes on the feeding of waders on Heron Island. *Sunbird* 6: 25-30

Evans, P.R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea* 64: 117-139

Evans, P.R., Herdson, D.M., Knights, P.J. & Pienkowski, M.W. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. I. Shorebird diets, invertebrate densities, and the impact of predation on the invertebrates. *Oecologia* 41: 183-206

Evans, P.R. & Smith, P.C. 1975. Studies of shorebirds at Lindisfarne, Northumberland, 2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. *Wildfowl* 26: 64-76

Feare, C.J. 1966. The winter feeding of the Purple Sandpiper. *Brit. Birds* 59: 165-179

Fuchs, E. 1975. Observations sur les ressources alimentaires et l' alimentation des Becasseaux variable, minute et cocorli *Calidris alpina, minuta* et *ferruginea* en Mediterranée, au passage et pendant l'hivernage. *Alauda* 43: w5-69

Goss-Custard, J.D. 1969. The winter feeding ecology of the Redshank *Tringa totanus*. *Ibis* 111: 338-356

Goss-Custard, J.D. 1970a. The responses of Redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *J.Anim.Ecol.* 39: 91-113

Goss-Custard, J.D. 1970b. Feeding dispersion in some overwintering wading birds. Pp 3-35 in Crook, J.H. (Ed.) *Social Behaviour in Birds and Mammals*. Academic Press, London & New York

Goss-Custard, J.D. 1973. Current problems in studying the feeding ecology of estuarine birds. *Coastal Ecology Research Paper* 4: 1-33

Goss-Custard, J.D. 1977a. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. *J.Anim. Ecol.* 46: 1-19

Goss-Custard, J.D. 1977b. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *J.Appl.Ecol.* 14: 721-739

Goss-Custard, J.D. 1977c. Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Anim. Behav.* 25: 10-29

Goss-Custard, J.D., Evans, P.R., Knights, P.J. & Pienkowski, M.W. in prep. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. 2. Changes in feeding ecology and foraging behaviour.

Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newbery, P.E. & Williams, R. le B. 1977. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *J.Appl.Ecol.* 14: 701-719

Goss-Custard, J.D., Jones, R.E. & Newbery, P.E. 1977. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *J.Appl.Ecol.* 14: 681-700

Goss-Custard, J.D., Kay, D.G. & Blindell, R.M. 1977. The density of migratory and overwintering redshank, *Tringa totanus* (L.), and curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. *Estuar.coast.mar.Sci.* 5: 497-510

Green, J. 1968. *The Biology of Estuarine Animals*. Sidgewick & Jackson, London

Green, G.H. & Summers, R.W. 1975. Snow Bunting moult in north-east Greenland. *Bird Study* 22: 9-17

Haukioja, E. 1971. Flightlessness in some moulting passerines in northern Europe. *Ornis Fenn.* 48: 101-116

Heppleston, P.B. 1971. The feeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland. *J.Anim.Ecol.* 40: 651-672

Hofmann, H. & Hoerschelmann, H. 1969. Nahrungsuntersuchungen bei Limikolen durch Mageninhaltsanalysen. *Corax* 3(19): 7-22

Hulscher, J.B. 1974. An experimental study of the food intake of the Oystercatcher *Haematopus ostralegus* L. in captivity during the summer. *Ardea* 62: 155-170

Hulscher, J.B. 1975. Het Wad, een overvloedig of schaars gedekte tafel voor vogels? Pp 57-82 in *Symposium Waddenonderzoek Uitgave van Stichting-Veth tot steun aan Waddenonderzoek.* Instituut voor Oecologisch Onderzoek, Arnhem

Hulscher, J.B. 1976. Localisation of Cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* 64: 292-310

Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72: 60-65

Knights, P.J. 1979. The effects of change in land use in some animal populations. Unpublished Ph.D thesis, University of Durham

Lasiewski, R.C. & Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23

Millard, A.V. 1976. The invertebrate faunas of *Spartina* marshes and their utilization by shorebirds at Lindisfarne, Northumberland. Unpublished Ph.D thesis, University of Durham

Millard, A.V. & Evans, P.R. MS. The use of exclosures to measure predation on intertidal invertebrates: problems resulting from movements of sediments and prey.

Minton, C.D.T. 1975. The waders of the Wash - ringing and biometric studies. Report of Scientific Study G of the Wash Water Storage Scheme Feasibility Study, to the Natural Environment Research Council

Moran, S. & Fishelson, L. 1971. Predation of a sand-dwelling mysid crustacean *Gastrosaccus sanctus* by plover birds (Charadriidae). *Marine Biology* 9: 63-64

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. 1975. *SPSS: Statistical Package for the Social Sciences.* 2nd ed. McGraw-Hill, New York

Norlin, Å. 1965. Zur Nahrungswahl von Limikolen in Schweden (Beobachtungsstation Ledskär). *Vogelwarte* 23: 97-101

Norton-Griffiths, M. 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher *Haematopus ostralegus* on the Edible Mussel *Mytilus edulis*. *Ibis* 109: 412-424

O'Connor, R.J. & Brown, R.A. 1977. Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia* 27: 75-92

Owens, N.W. & Goss-Custard, J.D. 1976. The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. *Evolution* 30: 397-398

Page, G. & Whitacre, D.F. 1975. Raptor predation on wintering shorebirds. *Condor* 77: 73-83

Payne, R.B. 1972. Mechanism and control of molt. Pp. 103-155 in D.S. Farner & J.R. King (Eds.) *Avian Biology* vol. 2. Academic Press, New York & London

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos* 15: 130-139

Pienkowski, M.W. 1972. Investigations on the Wash into factors affecting the distributions of some estuarine birds and their invertebrate prey species. Unpublished B.Sc. (Hons) dissertation, School of Biol. Sciences, Univ. of East Anglia.

Pienkowski, M.W. 1973. Feeding activities of wading birds and Shelducks at Teesmouth and some possible affects of further loss of habitat. Report to the Coastal Ecology Research Station, The Nature Conservancy (now Institute of Terrestrial Ecology)

Pienkowski, M.W. 1980. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Proc.Int.Waterfowl Research Bureau Symposium on Feeding Ecology, Gwatt, Switzerland, September 1977. *Verh.orn.Ges.Bayern* 23: in press

Pienkowski, M.W. & Dick, W.J.A. 1976. Some biases in cannon- and mist-netted samples of wader populations. *Ringing & Migration* 1: 105-107

Pienkowski, M.W., Knight, P.J., Stanyard, D.J. & Argyle, F.B. 1976. The primary moult of waders on the Atlantic coast of Morocco. *Ibis* 118: 347-365

Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26: 134-148

Prater, A.J. 1972. The ecology of Morecambe Bay III. The food and feeding habits of Knot (*Calidris canutus* L.) in Morecambe Bay. *J.Appl.Ecol.* 9: 179-194

Recher, H.F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* 47: 393-407

Schramm, M. 1978. The feeding ecology of Grey Plover on the Swartkops estuary. Unpublished B.Sc. (Hons) thesis, Department of Zoology, University of Port Elizabeth, South Africa

Smith, J.M.N. & Dawkins, R. 1971. The hunting behaviour of individual great tits in relation to spatial variations in their food density. *Anim.Behav.* 19: 695-706

Smith, J.M.N. & Sweatman, H.P.A. 1974. Food-searching behavior of titmice in patchy environments. *Ecology* 55: 1216-1232

Smith, P.C. 1975. A study of winter feeding ecology and behaviour of the Bar-tailed Godwit *Limosa lapponica*. Unpublished Ph.D thesis, University of Durham

Smith, P.C. & Evans, P.R. 1973. Studies on shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. *Wildfowl* 24: 135-139

Smyth, J.C. 1954. The study of wading birds in relation to the ecology of the sea-shore. *Act.Cong.Int.Orn.* 11: 529-531

Sokal, R.R. & Rohlf, F.J. 1969. *Biometry*. Freeman, San Francisco

Spitz, F. 1964. Repartition ecologique des anatidés et limicoles de la zone maritime du sud de la Vendée. *Terre et Vie* 18: 452-488

Summers, R.W. & Waltner, M. 1979. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. *Ostrich* 50: 21-37

Thomas, D.G. & Dartnall, A.J. 1971. Ecological aspects of the feeding behaviour of two calidritine sandpipers wintering in south-eastern Tasmania. *Emu* 71: 20-26

Vader, W.J.M. 1964. A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Neth.J.Sea Res.* 2: 189-222

Vielliard, J. 1973. Autoécologie comparée du Bécasseau variable *Calidris alpina* (L.). *Alauda* 41: 1-34

Wolff, W.J. 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. *Ardea* 57: 1-28

Zwarts, L. 1974. *Vogels van het brakke getijgebied, ecologische onderzoekingen op de ventsagerplaten*. Amsterdam

Paper 2. The foraging behaviour of Ringed and Grey Plovers in relation to the behaviour of their prey and environmental conditions

INTRODUCTION

Coastal wetlands are among the most productive of ecosystems and contain very dense populations of invertebrates in the intertidal flats (see, e.g. Whittaker 1970, Eltringham 1971, Milne & Dunnet 1972). Many of these invertebrates spend much of their time deep in the substrate either because of the physiological and/or feeding requirements (e.g. Green 1968) or to escape predation by fish and birds (cf Evans 1979). In the non-breeding season large flocks of arctic-breeding shore-birds resort to these areas to feed on the invertebrate fauna. The ways in which shorebirds forage for prey have been investigated by many workers (e.g. Drinnan 1958, Evans 1975, 1976, Goss-Custard 1969, 1976, 1977, Heppleston 1971, Hulscher 1976, Smith 1975, Smith & Evans 1973) but all these studies concentrated on those waders which forage largely by tactile means, as opposed to the plovers which apparently forage almost entirely by visual means. Few studies have been made of these, except by Burton (1974) who included Golden Plover *Pluvialis apricaria* in his study of anatomy, food and feeding behaviour of waders; Baker & Baker (1973) who included Semipalmated Plover *Charadrius semipalmatus* in their analysis of detailed behavioural sequences and habitat utilization by small waders; and Baker (1974) who looked at the foraging of migrant Black-bellied Plovers *Pluvialis squatarola*. In these studies, however, no attention was paid to the behaviour of the prey animals.

In Paper 1, the prey of Ringed and Grey Plovers *Charadrius hiaticula* and *Pluvialis squatarola* at Lindisfarne, Northumberland in the years 1973-76 was described. It was shown that the energy intake of plovers in the daylight hours fell steeply from autumn to mid-winter, at which time the rate of intake may not always have balanced requirements. The present paper documents the way in which plovers exploited the behaviour of some of their prey, considers how behaviours of both prey and predators varied with environmental conditions, and compares the foraging strategies of plovers and sandpipers.

STUDY AREA

Lindisfarne National Nature Reserve (Fig. 1) in north Northumberland comprises about 3240 hectares (12½ square miles), mainly of tidal mud- and sand-flats, saltmarsh and dunes.

Observations were made mainly on the eastern and northern parts of Holy Island Sands (abbreviated henceforth as HIS). This predominantly sandy area of about 750 hectares characterised by high densities of casts formed by lugworms *Arenicola marina* forms a wide strip between Holy Island itself and the muddier part of HIS, the Swad, which consists of about 1100 hectares covered with extensive beds of eelgrass *Zostera* spp. and some areas of cord-grass *Spartina* spp. In this paper, the sandy area is sometimes divided for reference purposes into the 'Low Flats' and the 'High Flats', separated by the 'Pilgrims' Way', a line of posts at about mid-tidal level.

The sandy region was the main winter feeding area of Ringed Plovers and one of the main areas used by Grey Plovers. The main prey of both species over most of the area were the polychaetes *Notomastus latericeus*, and, particularly for the Grey Plover, *Arenicola marina* (Paper 1).

Ringed Plovers were also watched in some sites just below the high water mark where they took small Crustacea, notably *Bathyporeia pelagica* and *Eurydice pulchra*, as their main prey, usually when lower areas were covered by water. These sites included the areas near the small salt marsh on the south side of the Snook and on the High Flats near the Sand Rig (Fig. 1).

Some observations were also made on the North Shore of Holy Island Snook (referred to henceforth as 'North Shore') where flocks of Ringed Plovers resorted on some occasions in winter and where a flock remained until it broke up progressively from February onwards as birds established pre-breeding territories. In these areas and around Old Law, Ringed Plovers also fed on sandhoppers *Talitrus* and flies, mainly *Coelopa* spp.

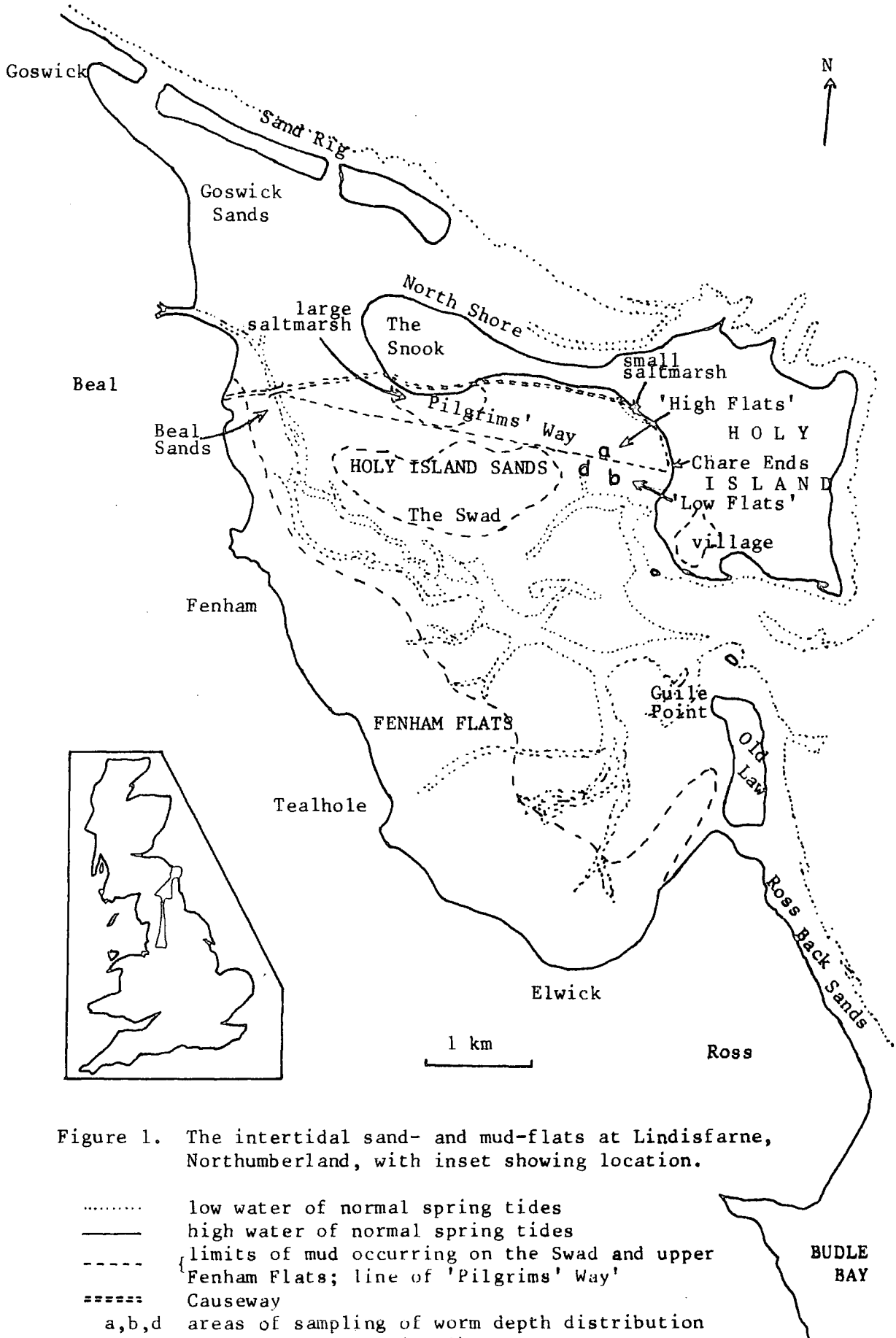


Figure 1. The intertidal sand- and mud-flats at Lindisfarne, Northumberland, with inset showing location.

.....	low water of normal spring tides
———	high water of normal spring tides
- - - - -	limits of mud occurring on the Swad and upper Fenham Flats; line of 'Pilgrims' Way'
======	Causeway
a,b,d	areas of sampling of worm depth distribution (see text and Fig. 2)

GENERAL DESCRIPTION OF FEEDING BEHAVIOUR

Both species of plovers generally fed while in loose flocks with individuals separated by about ½ m to over 50 m. Isolated individuals also occurred but, because of the nature of the flocks, the transition from flock to solitary feeding was often difficult to demarcate.

With a few exceptions noted later, plovers fed away from the water's edge, often spreading over much of the exposed inter-tidal sands. Areas where the surface had dried completely were, however, generally avoided, especially if wind started to blow the sand.

Both species feed in the highly characteristic stop-run-peck manner of plovers, presumably detecting prey visually rather than by touch. A bird stands still for up to several seconds depending on site, weather conditions and prey type (see later), before running rapidly to a new searching position or to peck at a prey item. The plovers' large eyes, set well to the sides of the head and commanding a wide angle of vision are presumably adaptations to foraging by night. Burton (1974) discusses how their short straight bills, large heads and related head anatomy aid rapid alignment over a site indicated by a short-term cue and are tolerant of hard impacts on the substrate. The detailed manner of taking particular prey species was described in Paper 1.

The distribution in waders' bills of Herbst corpuscles, which are pressure- and vibration-sensors, has been investigated by Bolze (1968). In some sandpipers many are concentrated in bony pits with openings directed towards the sources of pressure (allowing multiple layering and possibly the gathering of directional information). In the sandpiper family generally, corpuscles are found in fairly high densities spread along the outer bill. In contrast, plover bills do not have well developed pits and show concentrations of corpuscles only at the bill tip, but inside this as well as outside. The sandpiper pattern appears to be adapted to tactile prey detection and probing in the substratum whereas that of the plovers to surface pecking and sensitivity to precise gripping of prey as it is taken. Ringed Plovers and the other small sandplovers studied by Bolze had higher concentrations of Herbst corpuscles on the tip of the lower mandible

than the upper, as did the Lapwing. This might be expected as the lower mandible makes more contact with the ground as a bird pecks while reaching forward. Grey and Golden Plovers had similar densities on upper and lower mandibles, as seems appropriate for birds which take more prey from slightly further below the surface, and in which the pecking movements may be more nearly vertical.

The 'abortive pecks' described for Golden Plover by Burton (1974) in which pecks are arrested in mid-air, before contacting the ground, were recorded in both shore plovers in the present study but were infrequent. Also, both Grey and Ringed Plovers at Lindisfarne sometimes used the sideways flick combined with a peck (described by Burton) to send a piece of substrate flying to one side, presumably to expose and take prey.

In the 'up' waiting position adopted by both species the body was held somewhat more horizontally than that used by Golden Plovers (see, e.g., Burton 1974). This may be because the irregular surface of the feeding areas used by Golden Plovers requires a higher vantage point whereas the lower position of the inter-tidal plovers reduces the distance the head has to move to reach the prey.

A 'down' waiting position was also used, more by Grey Plovers than by Ringed Plovers (Table 1). It normally occurred in the sequence up-run-down-(run)-peck and presumably involved the localization of a cue first seen from a distance or the waiting for a second appearance of one seen from some way away. Golden Plovers feeding on pasture use the 'down' position more frequently (perhaps because of the greater cover for prey there) than when feeding on the shore (Burton 1974), where they use it at a similar rate to Grey Plovers. Foraging behaviour of Grey Plover at Lindisfarne also differed from that of Ringed Plovers in that, in any given set of conditions, 'ups' and 'runs' tended to take longer, 'runs' also covering greater distances (Table 1).

Ringed Plovers sometimes vibrated one foot on the substrate surface but this was rarely done by Grey Plovers.

TABLE 1. GENERAL COMPARISON OF SOME ASPECTS OF FORAGING BEHAVIOUR BY RINGED AND GREY PLOVERS AT LINDISFARNE

Given as mean ± S.E. (based on 345 observation cases on durations of activity for Ringed Plover and 315 for Grey Plover; and 184 & 98 observation cases on distances moved for the 2 species respectively).

	Ringed Plover	Grey Plover
Mean time in each 'Up' position (sec.)	1.95 ± 0.12	3.21 ± 0.19
Mean time for each 'Run→Up' (sec.)	0.70 ± 0.03	1.29 ± 0.05
Mean distance for each 'Run' (no. of paces)	3.16 ± 0.24	4.74 ± 0.25
" " " " " (m)	0.32	0.66
Mean no. of 'Downs' per minute	0.33 ± 0.05	1.23 ± 0.10
Occurrence of foot-trembling	18% of observations	one occasion only

The ways in which foraging behaviour varied in different tidal and weather conditions are considered later.

GENERAL METHODS

Invertebrate behaviour

To investigate depth distribution of invertebrates a modification of the technique used to estimate prey densities by sieving of mud samples was employed. Sampling corers were pushed rapidly into the sand and removed. Samples were then divided at pre-determined depths by metal plates pushed through slots on opposite sides of the corer. Each depth layer was then sieved and sorted separately. The method was not ideal in that vertical movement of animals could occur during the sampling even though the whole process took only a few seconds. While this may have affected the relative numbers in each layer, the method was probably sufficiently consistent to provide at least an index of changes in vertical distributions between samples.

Because of this technical problem, and the time involved in sorting samples, most effort was put into an alternative approach more directly related to the plovers' method of detecting prey, namely watching the sand surface for signs of prey activity. The general methodology was as follows. A wire quadrat was used to mark out a square of side 10 cm or 50 cm (depending on preliminary observation to indicate the levels of activity and the area which could be watched effectively). The observer knelt while counting the activity signs occurring in the quadrat over a timed period. Several tests indicated that the positioning of the observer had no appreciable effect on prey activity.

Bird feeding rate and foraging behaviour

Most observations were made using a 15x - 60x60 telescope from a car parked on the sand-flats and moved when necessary. Observations were timed by stop watches or by describing activities as they occurred on a tape-recorder running at constant speed. Substrate temperatures at about 2 cm depth, air temperature at about 10 cm above the ground and other weather conditions were noted throughout the observation period. Wind force was assessed on the Beaufort scale, cloud by eighths

of the sky covered, and rain on a subjective scale from 0 to 9.

At about 15 to 30 minute intervals the numbers of birds of each species in the area and the activities in which they were engaged (e.g. feeding, resting, preening) were noted. At similar intervals the distances between each plover in a flock and the nearest other bird of the same species was estimated in bird-lengths (19 cm for Ringed Plovers and 28 cm for Grey Plovers). Checks based on ciné-film of feeding birds and features in known positions indicated that such estimates were reasonably accurate and consistent.

The time periods between making the observations described above were spent in watching individual birds, usually for periods of about two minutes each. In each such 'case', the distance to the nearest other bird and the distance to the nearest individual of the same species were noted, as were its position and the size of flock in which it was, its age if apparent from plumage, individual identity if colour-ringed and the occurrence of 'foot-vibration'. The activity of the bird throughout the observation period was noted on the tape-recording as it occurred to give a sequence such as: "up, run, up, run, peck-success, run, up, peck-red-worm-bill-height, run, up".

The tapes were later replayed and a push-button operated as each activity was heard. This was linked to a pen-recorder which marked a paper roll travelling at 1 cm/sec so that the time for each activity could be measured off to an accuracy of 0.1 sec (see also below). The tape-recorder was then replayed, with stops as necessary, to note the activity relevant to each mark. The activities and their associated durations were then coded and transferred to punched card and thence to magnetic tape. Unfortunately this remarkably cumbersome and time-consuming method could not be replaced by a 'behaviour-organ' with a direct interface with a computer partly because of lack of resources but mainly because of the large number of different activities and prey types to be recorded and the speed at which these occurred; possibly a very high-speed typist or concert organist might have achieved this, provided that they had very fast reactions to unpredictable events - and a third hand to deal with the telescope.

A computer program 'PLOVPROG' (see Appendix 3 for details) was written to sort the coded data for each case, count frequencies of each activity and of simple sequences, calculate means and other basic statistics of handling times for various prey, times spent waiting or running, etc. The program also stored on magnetic tape for each case the frequency of each activity (or prey type or simple sequence) the total time spent in each of these activities and the sum of the squares of the times spent on each of these activities. Also recorded were the total time duration of the case and the total time during the case spent foraging (i.e. excluding any brief periods of time spent bathing, preening, fighting, etc.). The time spent foraging, rather than the total time duration of the case, was normally used in working out pecking rates, etc. The sorted data files were used as input for further analysis using the Statistical Package for the Social Sciences (Nie *et al.* 1975). Statistical treatments used in this paper follow Bailey (1959), Nie *et al.* (1975) and Sokal & Rohlf (1969).

Some observation cases were used to record the distances moved by the birds rather than the time spent in each activity. In these cases the number of paces made during each 'run' was recorded on the tape and the material was later treated in a similar fashion to that for timed data and analysed by PLOVPROG. As total time was also recorded the data could also be used for pecking rates, etc. in those cases in which all the time was spent foraging. Some further data were collected simply by counting the numbers of each peck and prey type in a noted time, this material being converted to the same data storage format by PLOVPROG. These different recording methods and the consequent varying restrictions on, and applicability of, their use accounts for the differences in sample size in apparently similar sets of conditions which will be used throughout this paper. Various checks have failed to indicate biases between sets of data collected in the same situation by the different recording methods.

Colour ciné-film was taken (at 24 frames per second) of birds feeding in the same natural situations, during the same observation periods as those in which some of the telescope observations were made. The film was used to check the validity of prey identification, as described in Paper 1. It was shown there that prey identification was valid,

if somewhat conservative, and correction factors to assign unidentified prey were calculated. It was also estimated that at least 90%, and probably 98%, of pecks resulted in a prey item being taken. Pienkowski (1973) found that 99.4% of 943 pecks by Grey Plovers at Teesmouth, County Cleveland, resulted in prey being taken.

Some of the same filmed material was used to test the validity and reliability of behavioural measures. The processed film was run at normal speed and data recorded on to tape as in the field and later analysed. This was repeated after an interval of several months. In this period many other birds were watched in the field and on film so that there was little likelihood of memory retention of previous assessments. After a further long interval, the film was analysed frame-by-frame. As explained in Paper 1, film analysis was a conservative assessment of observer ability as viewing conditions were less good by film than directly.

For Ringed Plovers the check using timed activities involved 178 activity events. Thirty-one (17%) differences between field-type recording and frame-by-frame analysis were revealed. In the 52 events for Grey Plovers, 6 (12%) differences were detected. However, in both species, all differences involved substitutions such as 'run, peck, up' for 'run, peck, run, up' and 'run, peck' for 'peck, run', generally when the birds were pecking rapidly. In such situations, the separation between peck (and the handling of prey) and preceding or following runs is somewhat artificial as small prey in particular may be taken while the bird is still moving. Comparison between the two field-type recordings of the same filmed data showed 8 (9%) differences for Ringed Plovers and 1 (4%) for Grey Plovers, all of the same type as those described above. The smaller numbers of discrepancies than with the frame-by-frame analysis indicates fairly consistent treatment in the field situation.

To overcome this problem of demarcation between 'pecks' and adjacent 'runs' a modification of 'PLOVPROG', 'PLOVP2'(see Appendix 3), was used to recode the data before PLOVPROG-type analyses were carried out. In PLOVP2, all runs which occurred immediately before or after a peck (of any outcome) were incorporated within that peck and their

times added to the duration of the peck as part of the pecking or handling time. If a run occurred between two pecks, it and its duration were included in the following peck (on the basis of both logic and subjective appearance of the behaviour). Runs not immediately before or after a peck (i.e. generally those between waiting positions) were unchanged. This resulted in all the discrepancies found in the film checks being eliminated. Unless otherwise stated, PLOVP2-type data was used for timed material in the following analyses.

The durations of activities as measured by the field-type analyses and frame-by-frame checks are compared in Table 2. There was no systematic significant difference in recorded duration times for either species between the two types of analyses or between the two field-type analyses. The maximum differences recorded were 0.5 sec and these generally related to activities of long duration. 80% of Ringed Plover field-type estimates and 90% of those for Grey Plover fell within 0.3 sec of the frame-by-frame analysis figures. For Ringed Plover, comparison between the two analyses of the same filmed data by the field-type method again showed slightly better agreement with each other than with the frame-by-frame check (79% within 0.1 sec and 94% within 0.3 sec).

A similar check using ciné-film was made on data collected in the field on distances travelled. Among sequences totalling 160 activities of Ringed Plovers, there were only 4 (2.5%) discrepancies and in 38 Grey Plover activities only 1 (2.6%). Comparison between the two field-type estimates showed 2 (2.5%) differences for Ringed Plovers and 1 (5%) for Grey Plovers. In all cases differences were of similar type to those for the timed data and generally resulted from a slight movement (less than a full length pace) being interpreted as a pace in one case but as no movement in another.

Comparisons of the distances moved (Table 2) indicate a general reliability of the method with no difference of more than 2 paces (these large ones being associated with longer runs) and about 90% within one pace. There did, however, appear to be a fairly consistent error in the field method in under-estimating distance moved by an average of less than one pace. This may have been associated with the

TABLE 2. COMPARISON OF DURATION OF ACTIVITIES AND LENGTHS OF RUNS BETWEEN ESTIMATIONS FROM FIELD-TYPE METHODS AND FRAME-BY-FRAME CINE ANALYSIS

	Parameter measured (1/10 sec or paces)															
	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	n	$\bar{x}$	s.e.	t	P
	Time difference - field-type minus frame-by-frame (1/10 sec)															
Ringed Plover	4	2	9	14	23	24	17	12	10	6	2	123	-0.043	0.47	0.09	n.s.
Grey Plover	1	1	4	5	11	6	5	3	1	1	1	39	-0.487	0.33	1.48	n.s.
	Time difference - between two field-type analyses (1/10 sec)															
Ringed Plover	0	1	0	5	8	32	10	3	1	1	2	63	0.175	0.19	0.92	n.s.
Grey Plover	1	0	1	2	3	6	1	1	2	0	1	18	-0.056	0.55	0.10	n.s.
	Distance difference - field-type minus frame-by-frame (paces)															
Ringed Plover	0	0	0	6	15	17	10	0	0	0	0	48	-0.354	0.14	2.59	<0.05
Grey Plover	0	0	0	2	5	3	0	0	0	0	0	10	-0.9	0.23	3.91	<0.01
	Distance difference - between two field-type analyses (paces)															
Ringed Plover	0	0	0	0	2	12	8	2	0	0	0	24	0.417	0.16	2.6	<0.05
Grey Plover	0	0	0	1	1	1	3	0	0	0	0	6	0	0.52	0	n.s.

problem discussed above of defining a pace.

Ciné-photography was also used to obtain measures impracticable in the field, such as the angles turned by the bird when moving to take prey, measures required to assess 'area searched'. The details of this assessment are given later.

Some observations were made at night, either using moonlight or an image-intensifier. The circumstances and limitations of these methods were discussed in Paper 1.

BEHAVIOUR OF THE MAIN PREY SPECIES AND THE PREDATORS' EXPLOITATION OF THIS

The main prey animals taken by plovers on HIS in daylight were *Arenicola marina*, *Notomastus latericeus*, *Scoloplos armiger*, *Bathyporeia* and *Eurydice*. The behaviour of *Arenicola* was studied in detail on HIS by Smith (1975) and is summarized below. Observations, made as part of the present study, on the smaller worms and amphipods are then detailed.

Arenicola

Arenicola usually lies at a depth of about 20 - 30 cm, but up to twice that depth in freezing conditions, in the horizontal gallery of its U- or L-shaped burrow. It makes excursions to the head shaft to feed and to the surface of the tail shaft to defaecate. Smith (1975) showed that Bar-tailed Godwits *Limosa lapponica* respond to the cue of cast formation to take *Arenicola*, their main prey. Most *Arenicola* were thus taken tail-first. My observations suggested that Grey Plovers also reacted to cast formation of *Arenicola* and 75% of *Arenicola* were taken tail first. The 25% head-first probably represent a much higher proportion taken in this manner than by godwits. It is not known if this reflects a greater sensitivity to more subtle cues by the large-eyed plovers or a speedier reaction to the presumably brief period of availability of prey in the head shaft (cf Burton 1974). In some cases, only the tails of *Arenicola* were taken. These were clearly distinguishable from whole small *Arenicola* as the latter showed the characteristic wide anterior and narrow posterior parts while the

former were very wide in relation to their length.

Smith (1975) found that the rate of cast formation by *Arenicola* increased approximately linearly from $-1^{o}C$ (below which no casts were formed) to $3^{o}C$ above which temperature the rate remained constant. At all temperatures the rate was somewhat higher on the falling tide than on the rising tide. On the flooding tide a higher proportion of casts occurred near the tide edge than on the ebb. (The tide edge was defined as the area covered by up to about 15 cm of water together with, on the ebb, that region above the edge retaining a thin layer of water and, on the flood, that region in which the rising water table reached the horizontal galleries.) On the flood tide, the proportion of casts occurring near the tide edge increased markedly at temperatures below $3^{o}C$. The period between defaecations of individual *Arenicola* increased progressively with time after exposure of the substrate and was longer in drier areas than wetter ones and on windy days than calm ones.

Notomastus and *Scoloplos*

Close examination of the surface of the mud in the area where plovers were seen to take red worms (invariably head-first) revealed a large number of small holes, the largest about 1 mm in diameter and most considerably smaller. The majority of these were found to be the openings of vertical burrows occupied by *Notomastus*, rather fewer by *Scoloplos*, and a small number by other worms, including *Phyllodoce maculata*, and the syphons of *Macoma* and *Cerastoderma*.

Most worms were found several centimetres below the surface (see below), so that the presence of holes was not a good indicator of the location of worms at the surface and therefore within reach of the plovers.

The only other possible cues that close inspection of the mud showed to occur with reasonable frequency were outflows of water from some of the holes. (In addition, very infrequently, the heads of *Notomastus* showed at the holes; the anterior parts of *Phyllodoce* extended from holes; and *Macoma* inhalent syphons were extended from their holes.) Although a small proportion of outflows were apparently due to *Macoma* or *Cerastoderma*, most appeared to be associated with the

presence of *Notomastus* or *Scoloplos* near the surface. This was investigated further by using a pair of forceps to 'peck' at 50 holes as water flowed from them and 50 similar nearby holes from which there was no flow at that time (Table 3). Sixty-eight percent of 'pecks' at outflows resulted in the capture of a worm compared with only 22% at other holes. It is likely that plovers pecking at outflows would perform even better because of their speed of response, better shaped extraction device (bill rather than forceps), and less clumsy handling of it. Because of the absence of other visual cues and the reliability of outflows as indicators of available worms, I consider that these were the cues being used by plovers to detect *Notomastus* and, to a lesser extent, some other prey.

Smith (1975) considered that Bar-tailed Godwits at Lindisfarne detected small polychaetes by tactile means while probing in the substrate and he investigated the depth distribution of the worms by sampling the substrate. Almost all worms were found within 15 cm of the surface, 28% to 55% (according to temperatures) being in the top 5 cm. There were indications that at 4 to 7°C, the proportion in the top 5 cm was highest on the ebb tide-line (55%), next highest on the flood tide-line (49%), then on wet areas above the tide-line (41%) and finally on drier areas (36%). On colder days, the percentages were lower: 43% on the ebb tide-line at 2°C and 28% on the flood tide-line at -1°C. However, because of high variances, these differences were not statistically significant.

These aspects were investigated further in the present study using a similar sampling method to that used by Smith. On 21 February 1976 when the sand temperature was 6°C, samples were taken at about 5 min intervals throughout the period of tidal emersion on the main study area of HIS. Five 10 x 10 cm samples were taken randomly from each of three areas (Fig. 1), one set from area a (just above the Pilgrim's Way), the others from area b (Grey Plover Flats) and area d (Godwit Creek). The surface of area b dried more rapidly than of area d. Samples were returned to the kitchen, sieved and sorted as described in Paper 1.

The proportion of *Notomastus* in the top 5 cm was very variable

TABLE 3. OUTFLOWS FROM HOLES AS INDICATORS OF WORMS (PRINCIPALLY *NOTOMASTUS*)

	Holes with outflows	Holes without outflows	Total
Worm present	34	11	50
No worm	16	39	50
Total	50	50	100

$\chi^2_1 = 21.38$ $P << 0.001$

in all areas (Fig. 2) but was, on average, twice as high in the wet area d as in the drier area b (mean values, using the arcsine transformation (to covert percentages to values conforming to Normal Distribution requirements), 69.3% and 34.7%, respectively). This difference was highly significant ($t_{45} = 4.73$, $P < 0.001$). No tidal pattern of depth distribution was apparent during most of the period of exposure in area d, but the proportion in the surface layers in area b declined somewhat during the period of emersion. In both areas the proportion near the surface increased slightly just before tidal immersion. The last set of samples taken from area d showed a significant increase in proportion (90.7%) in the top 5 cm compared with all other samples taken during low water in the same area (62.0%) ($t_{21} = 2.61$, $P < 0.02$). These patterns are compatible with those found by Smith (1975).

As plovers appear to use visual, rather than tactile, foraging methods, further investigations of invertebrate availability used measures of the presumed visual cues - the outflows of water - rather than samples of the substrate to indicate the densities of available prey. Observations were made by kneeling on the mud and watching from about 30 cm height an area of mud marked by a 10 cm x 10 cm quadrat for a period of 2 min. Four sites were used, all in area b on Grey Plover Flats of HIS (which held high densities of the worms). Sites A and B were on wetter areas than sites C and D, but worm densities were fairly similar in the two areas.

At all sites the number of outflows observed in 2 min. intervals increased significantly with increasing temperature (Fig. 3). The difference in slopes between sites A/B and C/D are presumably due to local conditions. On three occasions the rate at which outflows occurred was investigated in relation to tidal time (Fig. 4). There was some tendency, particularly in the wetter areas, for the rates to increase slowly after emersion. Worm activity probably did not increase over this period, but outflows became more visible as the surface film of water dried out. A decrease in the rate at which outflows were seen often occurred in the later part of the exposure period. This appeared to be associated with progressive drying of the surface of the substrate. However, in some cases an increase in rate was noticed immediately before tidal covering.

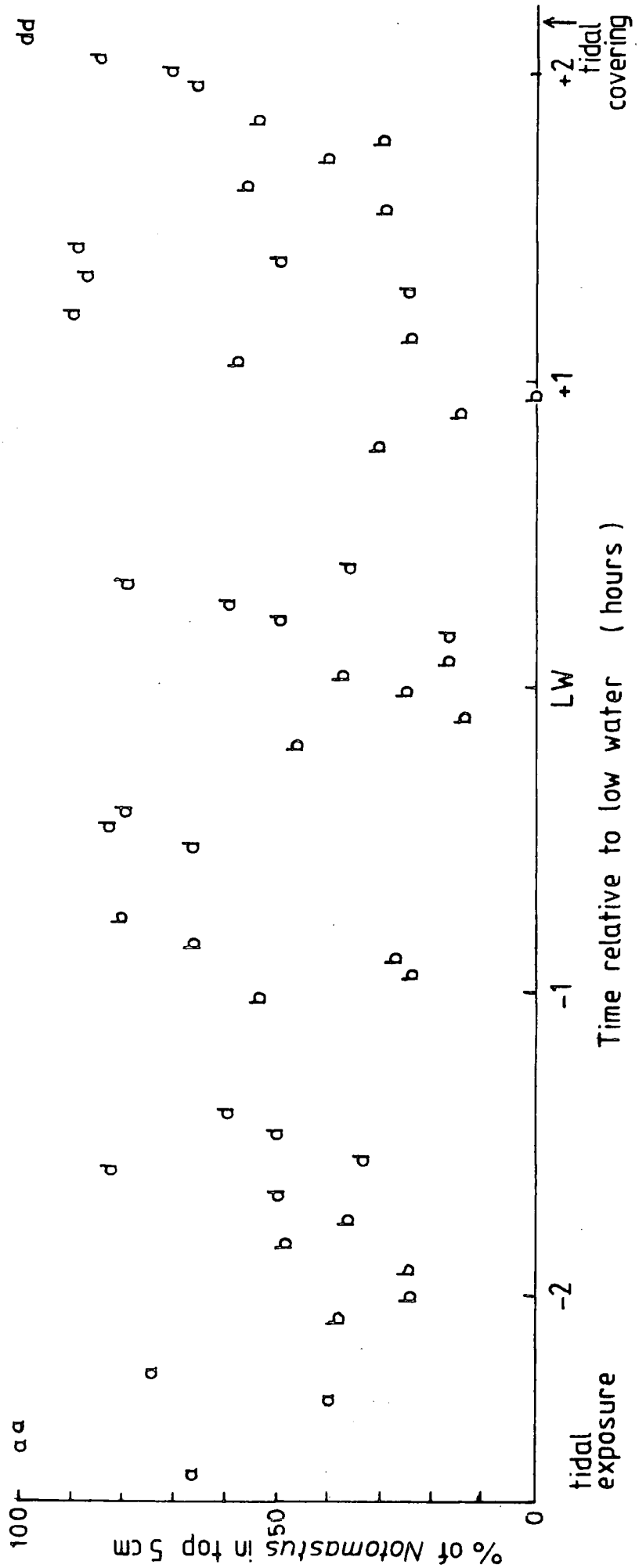


Figure 2. Percentage of *Notomastus* in top 5 cm of sand on 21 February 1976.

Samples taken from area a (above Pilgrims' Way), b (Grey Plover Flats), and d (Godwit Creek)

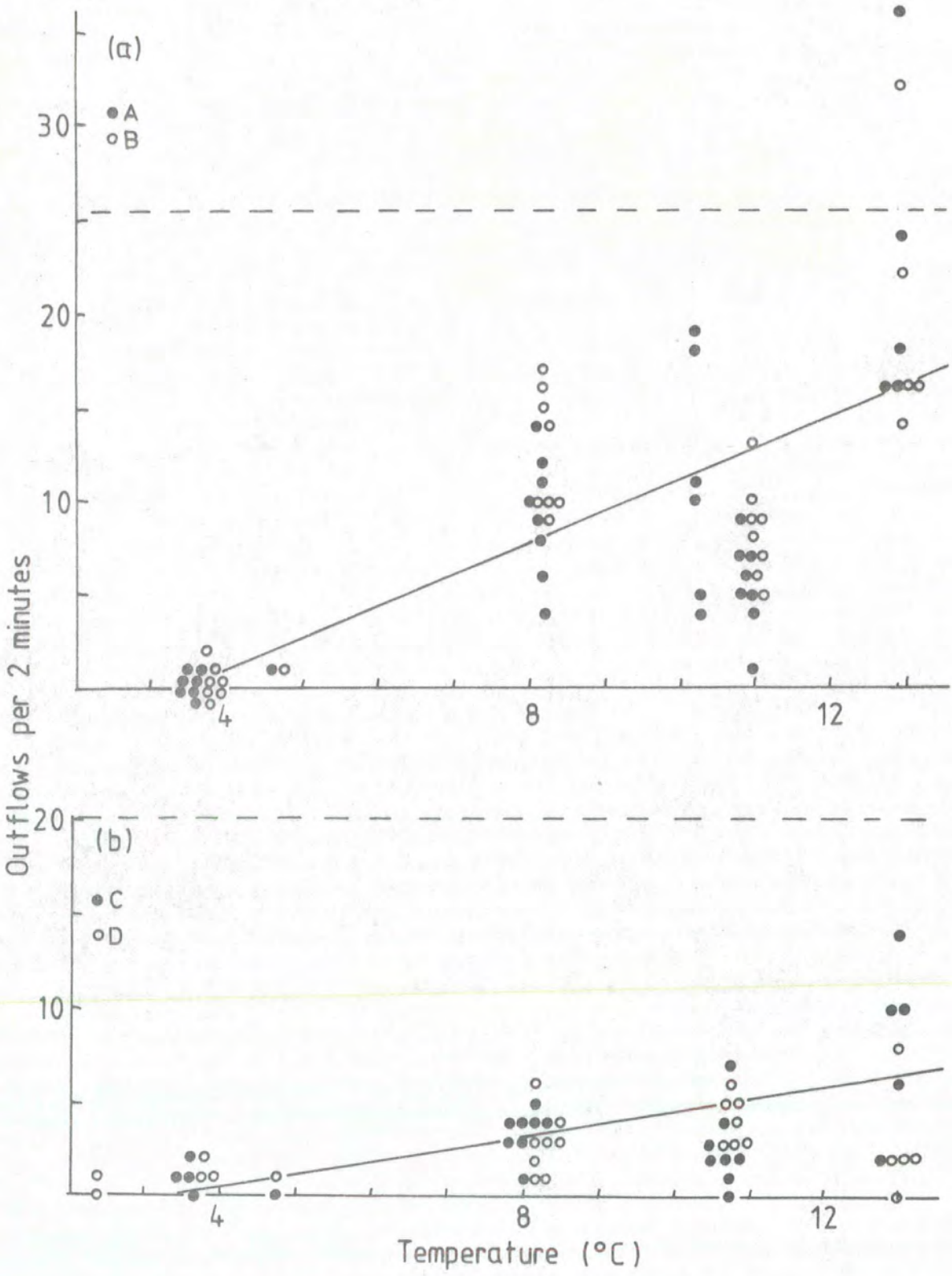


Figure 3. Outflows from holes per 2 minutes in 100 cm^2 areas in relation to sand temperature. (a) sites A & B, (b) sites C & D

Fitted regression lines are (a) $y = 1.69x - 5.82$, $P < 0.001$; and
(b) $y = 0.67x - 2.2$, $P < 0.01$

Dashed lines indicate outflows which would be produced if all worms in area of this estimated density produced one outflow during the observation period.

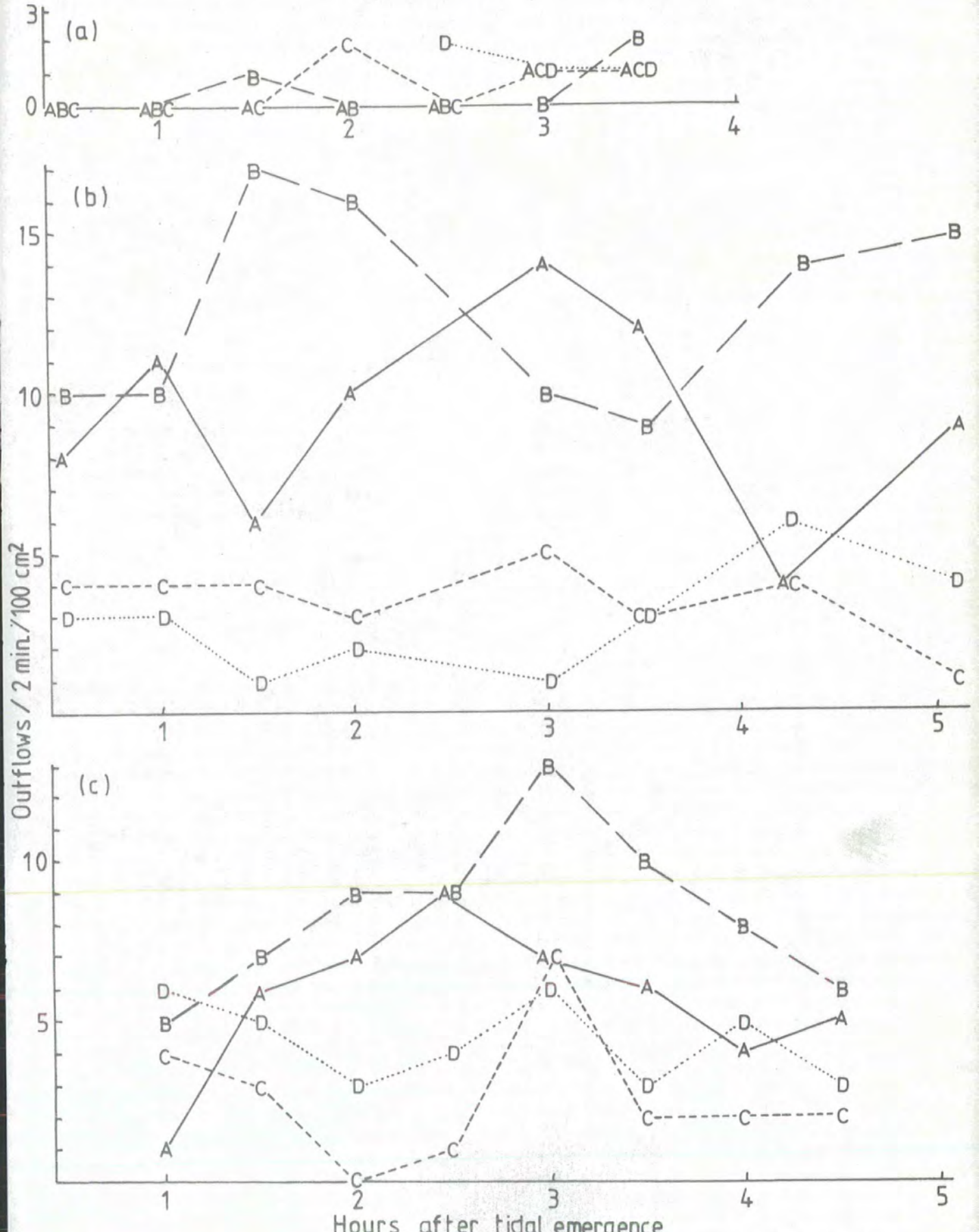


Figure 4. Outflows from holes per 2 minutes in 4 100 cm^2 areas (A,B,C,D) in relation to time after tidal emergence, on different days when the sand temperatures were (a) 3.7°C; (b) 8.2°C; and (c) 10.8°C.

All these data were recorded on days of wind-force 5 or below. Attempts were made to record worm activity at high wind speeds, but increasing movement of any surface films of water made counting outflows impracticable. In such conditions, areas without surface water dried rapidly. In all wind conditions, although activity remained visible in damp areas, if the surface dried completely, so that sand particles moved if a wind blew, no outflows were apparent, perhaps because water soaked into the sand below the surface. However, it was probably due mainly to a real reduction in activity.

Observations in rainy conditions were also impracticable because the distinction between outflows and impacting rain-drops was difficult to make.

Crustacea and other invertebrates on the high flats

The activity of small invertebrates on the high tidal level flats was investigated by watching areas enclosed by 50 x 50 cm quadrats for periods of 15 or 30 sec. These animals were not visible unless they moved. Since these high level areas were those where 'foot-vibration' by Ringed Plovers was most frequently observed, after each period of observation a second observation of 15 or 30 sec duration was made, during which a pair of forceps was vibrated on the surface of the sand to simulate foot-vibration by the plover.

On the Sand Rig feeding site used by Ringed Plovers, no activity of any invertebrates was apparent at 4°C but some at 13°C and more at 17°C (Fig. 5a). In both of the warm conditions, significantly more animals were seen during "vibrations" than without. Almost all animals seen were *Eurydice*.

On high HIS, near the small salt-marsh, a similar pattern of activity in relation to temperature was found (Fig. 5b), no crustacea being visible at -1.5°C, few at 4°C and more at 13°C and 17°C. At 4°C and 13°C, significantly more animals, about half of which were *Bathyporeia* and half *Eurydice*, were seen during vibrations than without. At 17°C also more were visible during vibrations, but the difference was not significant. At -1.5°C, the only animals visible were two very small thin worms (less than 4 mm long), which moved in response to

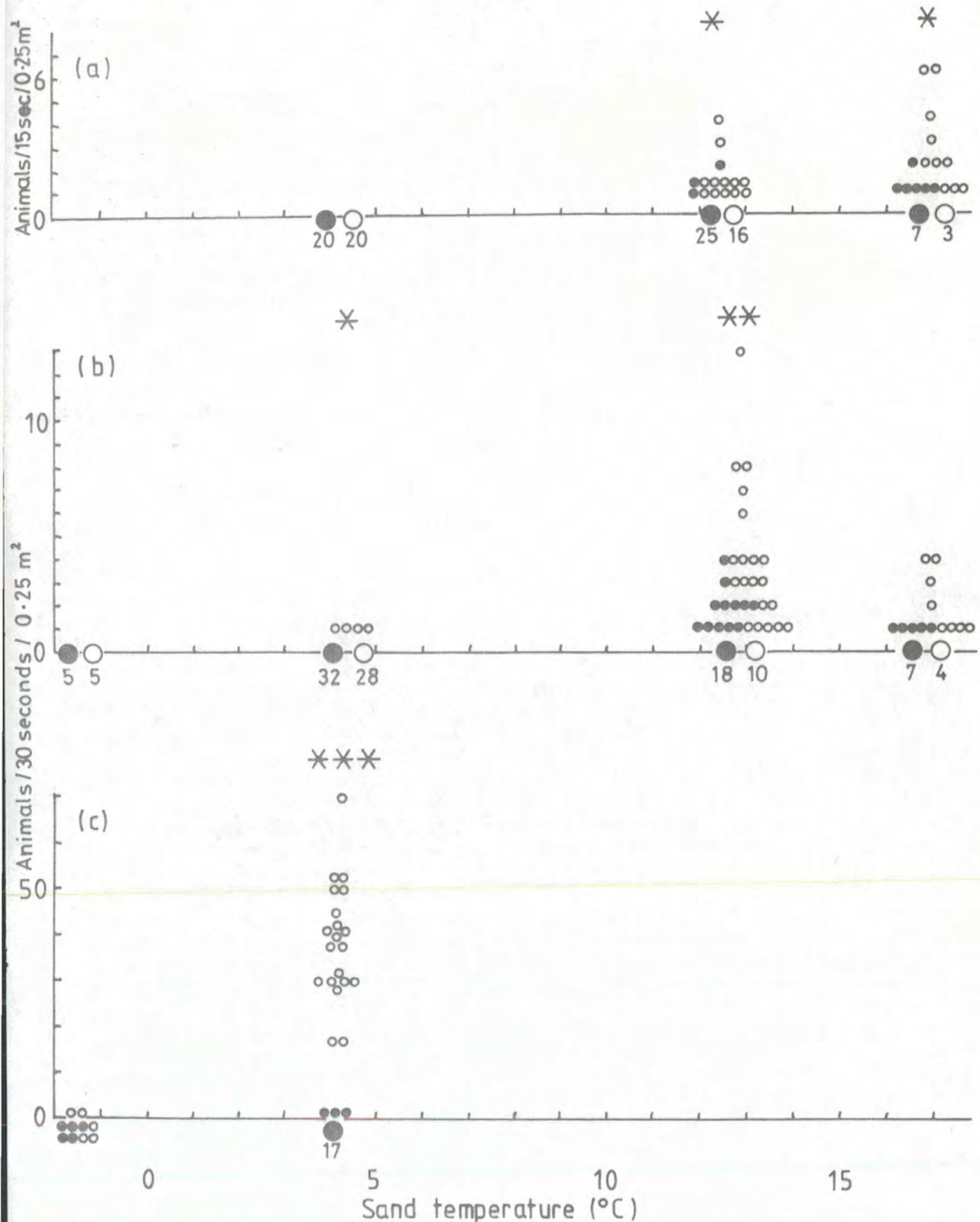


Figure 5. Small prey observed in relation to temperature and vibration. (a) small crustacea near Rig; (b) small crustacea near small salt marsh; (c) very small worms near small salt marsh. o = with vibration, ● = without vibration (large circles represent the numbers of points indicated below them). Significant differences between with vibration and without indicated by: ✳ (5%); ✳✳ (1%); ✳✳✳ (0.1%)

vibration. At 4°C, many more of these worms were seen, almost all during vibrations (Fig. 5c). It is doubtful, however, that these were taken by feeding plovers as the worms became visible only in the immediate vicinity of the vibrating tip of the forceps (never more than 1 cm from this). Plovers normally peck further from their feet than this and did not concentrate their pecks in this immediate area. (Activity of these worms was not investigated at higher temperatures.)

Night

Few night observations were made. On one occasion when the temperature was about 10°C and the sky overcast both before and after dusk, the number of outflows seen in each 2 min. interval was similar in daylight and at night. However, at night *Phyllodoce* emerged from the sand to a length of several centimetres and fed in water-filled hollows. Such emergences were rarely observed in daytime. At night during 25 two minute observation periods on 100 cm^2 areas, 1 *Phyllodoce* was seen in each of two areas and three in a third. The worms remained active throughout the nocturnal observation periods and later checks showed that they were still active on the surface about 30 min. later. Thus, unlike *Notomastus*, *Phyllodoce* remained on the surface, and appeared unaffected by torch-light. Small sections of some of the *Phyllodoce* were luminous, perhaps because of the presence in their guts of diatoms and dinoflagellates. These are common on the mud surface and luminesce when disturbed.

FEEDING RATES AND ENVIRONMENTAL CONDITIONS

Ringed Plovers on the low tidal level flats

On the Low Flats at least 65% of the prey items taken by Ringed Plovers were thin worms (Paper 1). The estimated number of thin worms taken per minute, as defined in Paper 1, are considered below in relation to environmental conditions. (Rates of capture of all prey, and estimated maximum and minimum rates of taking worms gave generally similar relationships.)

Prey capture rate rose with rising mud temperature up to about 6°C, above which the rate decreased (Fig. 6). At any given temperature, no seasonal variation in the rate of capture of thin worms could be

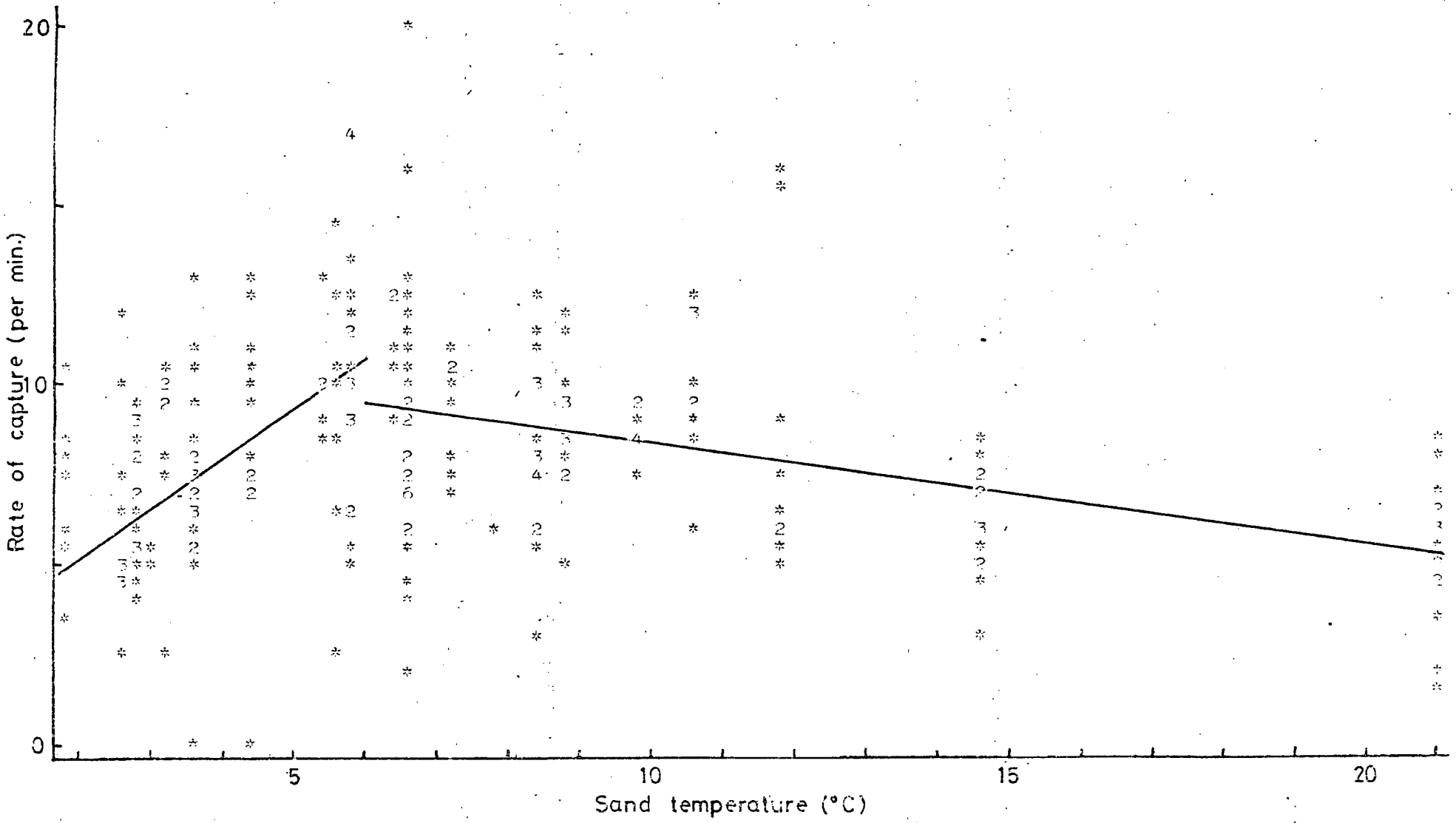


Figure 6. Estimated rate of capture of thin worms by Ringed Plovers on the Low Flats in relation to sand temperature during observations. Fitted regression lines are: $y = 1.19x + 3.65$ ($P<0.001$) below $6^{\circ}C$ and $y = 11.03 - 0.27x$ ($P<0.001$) above $6^{\circ}C$.

Note : On this and similar figures, single points are represented by asterisks, 2 to 8 coincident points by the number of such points, and 9 or more coincident points by '9'.

established. The capture rate was inversely related to wind force at low temperatures but directly related at high ones (Table 4.) At low temperatures only, capture rates increased significantly with increasing cloud cover and, at higher temperatures only, feeding rate declined significantly with time after high water.

As some of the independent variables considered above were correlated with each other, stepwise multiple regression analysis was used to examine the relationships further (Table 4). Rainfall was not included in this analysis because its scoring method was non-linear and its effects on prey availability could not be measured. Because there was also a non-linear relationship between worm capture rates and mud temperature, data collected below 6°C were treated separately from those from higher temperatures. The rate of capture of red worms showed a significant partial correlation only with mud temperature, accounting for 27% of the variance at the lower temperature conditions and 19% at higher ones. Inclusion of other environmental variables in the regression equation increased these figures to 28% and 20% respectively. (Note that lower significance levels in the multiple regression analyses resulted partly from the reduction in sample size, as only those cases were included in which data for all variables rather than pairs of variables, were available. Thus the results of the multiple regression analyses may be over-conservative. However, they do not differ greatly from those of simple regression.)

The mean size of worms taken increased significantly with increasing temperature and time after high-water, the former remaining significant in multiple regression analyses (Table 4).

Ringed Plovers on the high tidal level flats

On the main feeding area used during the higher part of the tidal cycle, namely the High Flats near the road and small salt marsh, thin worms and other small prey, mainly *Bathyporeia* and *Eurydice*, formed most of the diet (Paper 1).

Significant relationships similar to those found on the Low Flats were established for the estimated rate of capture of thin worms in relation to mud temperatures (Fig. 7) and wind force, these

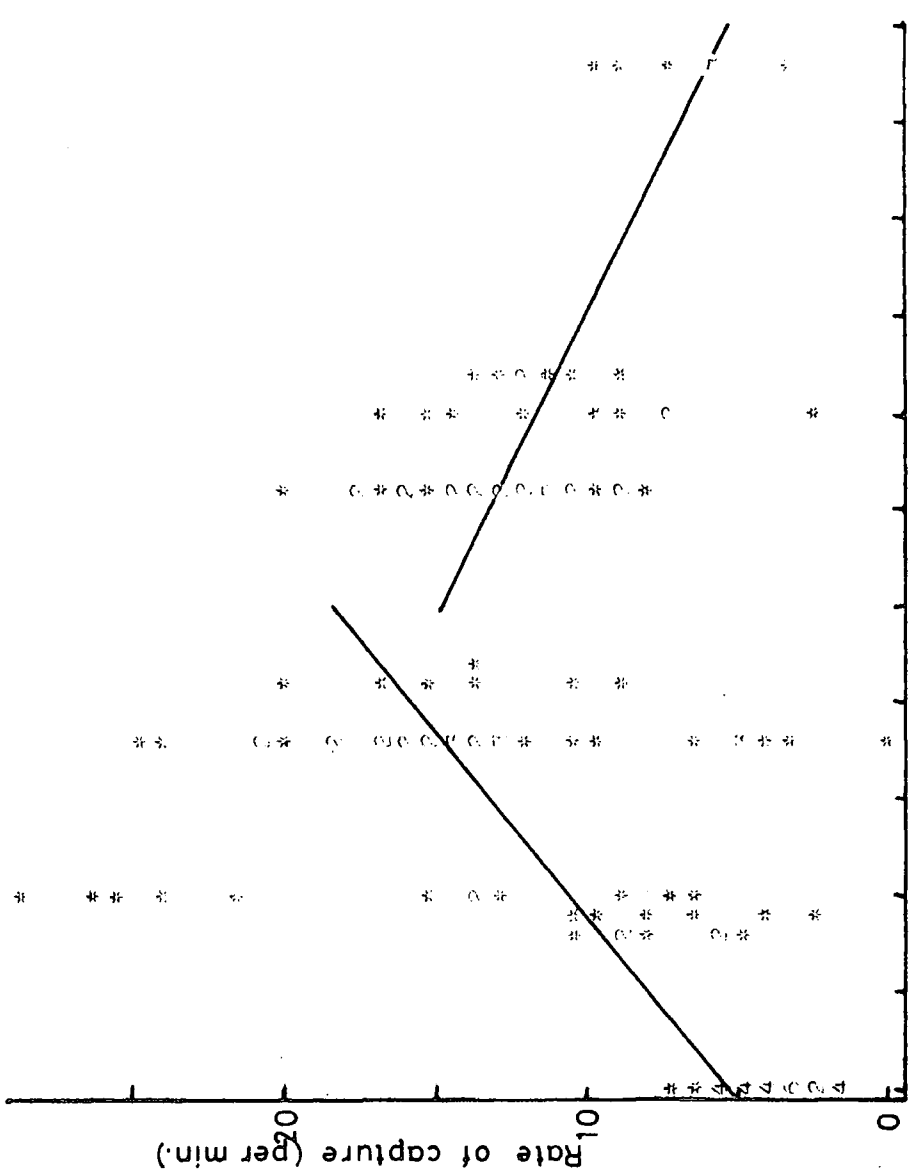


Figure 7. Estimated rate of capture of thin worms by Ringed Plovers on the High Flats in relation to sand temperature.
Fitted regression lines are: $y = 2.28 + 2.59x$ ($P < 0.001$) below $6^{\circ}C$
and $y = 24.0 - 1.54x$ ($P < 0.001$) below $6^{\circ}C$

TABLE 4. RELATIONSHIPS BETWEEN FEEDING RATES AND ENVIRONMENTAL CONDITIONS

For significant relationships, the correlation coefficient is given and the level of significance (<0.05, 0.01, 0.001) indicated after it by 1 to 3 asterisks. For those relationships which remained significant in stepwise multiple regression analysis, significance levels in that analysis are indicated before the coefficient. (Rain was not included in multiple regression).

(ne = not examined; ni = not included; - = examined but not significant)

	RINGED PLOVER				GREY PLOVER			
	Low flats		High flats		Low flats		High flats	
	<6 °C	≥6 °C	<6 °C	≥6 °C	Aug to Feb	Mar to May	<5.5°C	≥5.5°C
Rate of taking *Arenicola*								
Mud temperature	ne	ne	ne	ne	-	** 0.30**	-	-
Wind force	ne	ne	ne	ne	-	-0.20*	-0.31**	-
Rain	ne	ne	ne	ne	-	-	-	-
Cloud	ne	ne	ne	ne	-	* 0.19*	-	-
Time after high water	ne	ne	ne	ne	-	-0.30**	-	-
Rate of taking thin worms								
Rate of taking *Arenicola*	ni	ni	ni	ni	-0.17**	-0.37**	-	*-0.25**
Mud temperature	** 0.47**	**-0.43**	* 0.58**	**-0.59**	0.40**	**-0.48**	-	-
Wind force	-0.19**	0.23**	**-0.37**	** 0.52**	-0.25**	0.22*	-	-
Rain	-	-	-	-	-0.20**	-	-	-
Cloud	0.19**	-	-	-	-	-	-	-
Time after high water	-	-0.18*	-0.39*	-	** 0.32**	** 0.48**	-	* 0.26**
Rate of taking small prey								
Rate of taking *Arenicola*	ne	ne	ni	ni	ne	ne	ne	ne
Mud temperature	ne	ne	0.53**	**-0.41*	ne	ne	ne	ne
Wind force	ne	ne	**-0.32**	0.34*	ne	ne	ne	ne
Rain	ne	ne	-	-	ne	ne	ne	ne
Cloud	ne	ne	-	-	ne	ne	ne	ne
Time after high water	ne	ne	-0.33**	-	ne	ne	ne	ne
Length of visible thin worms taken								
Rate of taking *Arenicola*	ni		ni		-	-0.27**	-	
Mud temperature	* 0.13*		-		-	-0.19*	**-0.28**	
Wind force	-		-		-	-	** 0.28**	
Rain	-		-		-	0.24**	-	
Cloud	-		-		-	-	** 0.23**	
Time after high water	0.10*		*-0.24**		** 0.21**	** 0.41**	* 0.12	

remaining significant in multiple regressions analysis (Table 4). At low temperatures, capture rate also declined with time after high water. This is investigated further below. Mean size of worms captured was higher (but not quite significantly so, probably due to small sample size) at higher temperatures but fell significantly with time after high water.

The number of pecks in unit time, less the estimated rate of capture of thin worms, was used as a measure of the rate at which birds attempted to catch small prey, principally *Bathyporeia* and *Eurydice*. If all attempts were successful, this rate is equivalent to the maximum possible rate at which small items were captured. A minimum rate of capture, based on only those small items seen to be taken, gave generally similar relationships to the maximum estimate in comparisons with environmental conditions.

The estimated rate of pecking at small prey showed a pattern similar to that for thin worms in relation to temperature, increasing with temperature to about 6°C, but declining above that (Fig. 8). At a given temperature no seasonal differences in pecking rate could be found. The rate of pecking at small prey showed similar relationships with wind force and time after high water as did the rate of capture of thin worms (Table 4).

Because few birds fed in this area between HW + 3.5 h to HW + 9 h (when most birds were on the Low Flats), the feeding rates here were also investigated separately for ebb and flow (Table 5). The rates of capture of worms and small prey varied in parallel in relation to environmental conditions. At high temperatures no differences in rates between ebb and flow tides were significant but at low temperatures feeding rates on the ebb were significantly higher than on the flow. During the flow tide period, the rates of prey capture increased towards high water (e.g. Fig. 9), and, possibly but less clearly, during the ebb the rates decreased.

At low temperatures feeding rates were also higher with onshore than with offshore winds (Table 6), but again this did not apply at temperatures above 6°C. This may be because onshore winds

TABLE 5. FEEDING RATES OF RINGED PLOVERS AT HIGH TIDAL LEVELS IN RELATION TO MUD TEMPERATURE AND TIDAL STATE

	High flats			North Shore		
Temperature	all	<6 °C	≥6 °C	all	<6 °C	≥6 °C
Estimated rate of taking thin worms						
ebb	12.5 ± 0.8(61)	13.6 ± 1.1(38)	10.8 ± 0.9(23)	8.2 ± 0.4(102)	7.7 ± 0.5(70)	9.3 ± 0.7(32)
	$t_{158} = 4.14^{***}$	$t_{112} = 5.00^{***}$	$t_{44} = 1.13$ ns	$t_{166} = 2.02^{*}$	$t_{112} = 1.71$ ns	$t_{51.29} = 1.40$ ns
flow	8.7 ± 0.5(99)	7.7 ± 0.6(76)	12.0 ± 0.6(23)	6.9 ± 0.4(66)	6.3 ± 0.6(44)	8.2 ± 0.5(22)
Estimated rate of taking small prey						
ebb	10.8 ± 0.8(61)	11.3 ± 1.0(38)	9.9 ± 1.1(23)	6.2 ± 0.4(102)	6.1 ± 0.5(70)	6.4 ± 0.8(32)
	$t_{158} = 3.22^{**}$	$t_{112} = 4.27^{***}$	$t_{44} = 1.66$ ns	$t_{164.46} = 3.09^{**}$	$t_{111.33} = 2.42^{*}$	$t_{38.78} = 1.96$ ns
flow	7.7 ± 0.6(99)	6.4 ± 0.6(76)	12.2 ± 0.8(23)	4.6 ± 0.3(66)	4.5 ± 0.4(44)	4.8 ± 0.3(22)

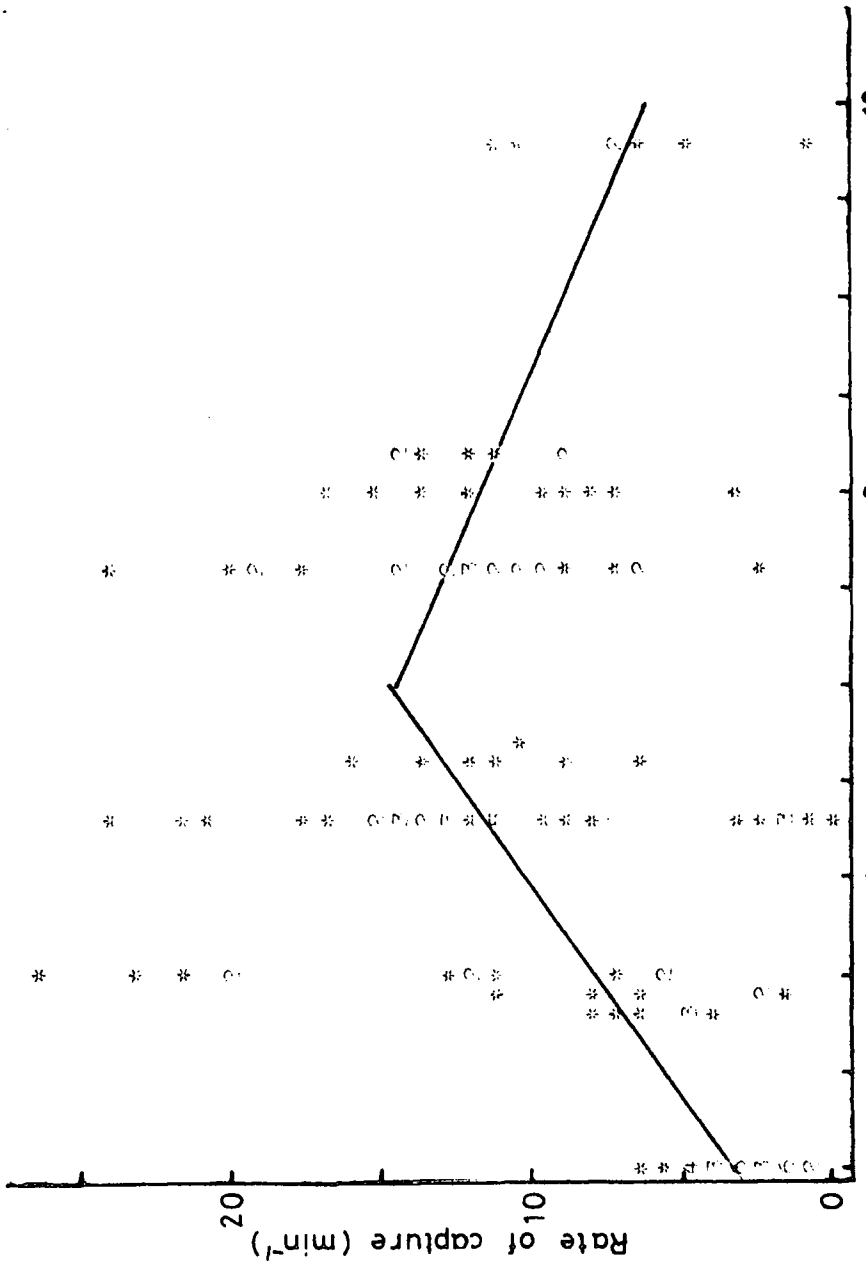


Figure 8. Estimated rate of capture of small prey by Ringed Plovers on the High Flats in relation to sand temperature.

Fitted regression lines are: $y = 1.01 + 2.17x$ ($P < 0.001$) below $6^{o}C$
and $y = 21.6 + 1.29x$ ($P < 0.001$) above $6^{o}C$

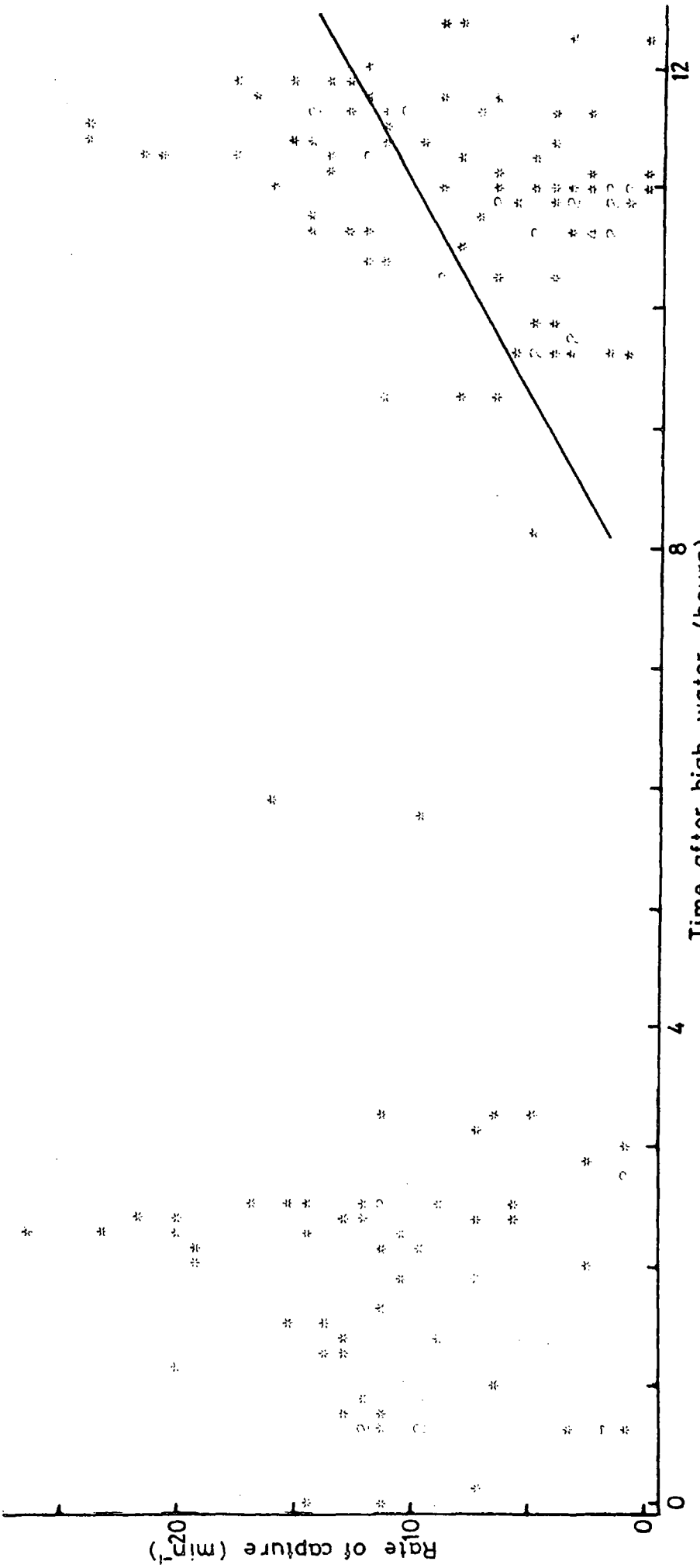


Figure 9. Estimated rate of capture of small prey by Ringed Plovers on the High Flats in relation to time after high water.

Regression line fitted to cases on flow tide is: $y = 2.73x - 20.34$ ($P < 0.001$)

TABLE 6. FEEDING RATES OF RINGED PLOVERS AT HIGH TIDAL LEVELS IN RELATION TO MUD TEMPERATURE AND WIND DIRECTION

SE - W winds are onshore on the High Flats and offshore at the North Shore

	High Flats			North Shore		
Temperature	all	<6 °C	≥6 °C	all	<6 °C	≥6 °C
Estimated rate of taking thin worms						
wind SE - W	12.4 ± 0.7(80)	12.5 ± 0.8(73)	11.5 ± 0.7(7)	7.1 ± 0.5(61)	6.9 ± 0.5(57)	9.7 ± 2.4(4)
	$t_{140} = 3.91^{***}$	$t_{97.85} = 9.32^{***}$	$t_{37} = 0.65$ ns	$t_{142} = 1.88$ ns	$t_{94} = 1.39$ ns	$t_{46} = 0.78$ ns
wind NW - E	8.6 ± 0.6(62)	4.9 ± 0.4(30)	12.4 ± 0.6(32)	8.3 ± 0.4(83)	8.1 ± 0.8(39)	8.5 ± 0.5(44)
Estimated rate of taking small prey						
wind SE - W	10.7 ± 0.7(80)	10.5 ± 0.7(73)	11.9 ± 1.0(7)	5.4 ± 0.4(61)	5.2 ± 0.4(57)	7.4 ± 1.3(4)
	$t_{140} = 2.81^{**}$	$t_{100.17} = 8.2^{***}$	$t_{37} = 0.00$ ns	$t_{142} = 0.03$ ns	$t_{59.04} = 0.95$ ns	$t_{46} = 2.11^{*}$
wind NW - E	7.9 ± 0.7(62)	3.7 ± 0.4(30)	11.9 ± 0.9(32)	5.4 ± 0.4(83)	6.1 ± 0.8(39)	4.7 ± 0.4(44)

concentrate the small Crustacea at high tidal levels. At high temperatures, prey activity may be sufficient in any wind direction to allow maximum pecking rates.

Tables 5 & 6 include similar comparisons for prey capture rates on the North Shore. Here the difference in capture rates between ebb and flow tides was less than on HIS. Wind direction had little effect. Rates of prey capture on the North Shore only exceeded those on HIS high flats when winds were from NW to E and temperatures low.

Grey Plovers on the low tidal level flats

The diet of Grey Plovers on HIS consisted mainly of *Arenicola*, which contributed most of the biomass by virtue of its large size, and thin worms, of which a large number were taken (Paper 1). Because of the low frequency at which *Arenicola* were taken, the number taken in most observation cases was zero, particularly in autumn and winter. In these seasons the non-zero records were too few to allow investigation of relationships between capture rate and environmental conditions. In spring, (March to May inclusive), however, more *Arenicola* were taken at higher mud temperatures (Fig. 10), and under increasing cloud cover (Table 4) but fewer with increasing wind force and time after high water (Fig. 11).

For Grey Plover, as for Ringed Plover, the various measures (maximum, estimate and minimum) of rate of capture of thin worms generally followed the same patterns of variation in relation to environmental factors. Only the estimated rates are used hereafter.

The pattern of variation in rates of capture of thin worms differed seasonally. In spring, capture rate fell with increasing temperatures (Fig. 12), rose with increasing wind strength (Table 4) and time after high water (Fig. 13). Rates of capture of thin worms were also related inversely to rate of capture of *Arenicola* (Fig. 14).

In autumn and winter, the opposite relationships were found between rates of capture of thin worms and wind strength or temperature, but similar ones with tidal time and rate of capture of *Arenicola* (Table 4). The rates also fell with increasingly heavy rain. (A

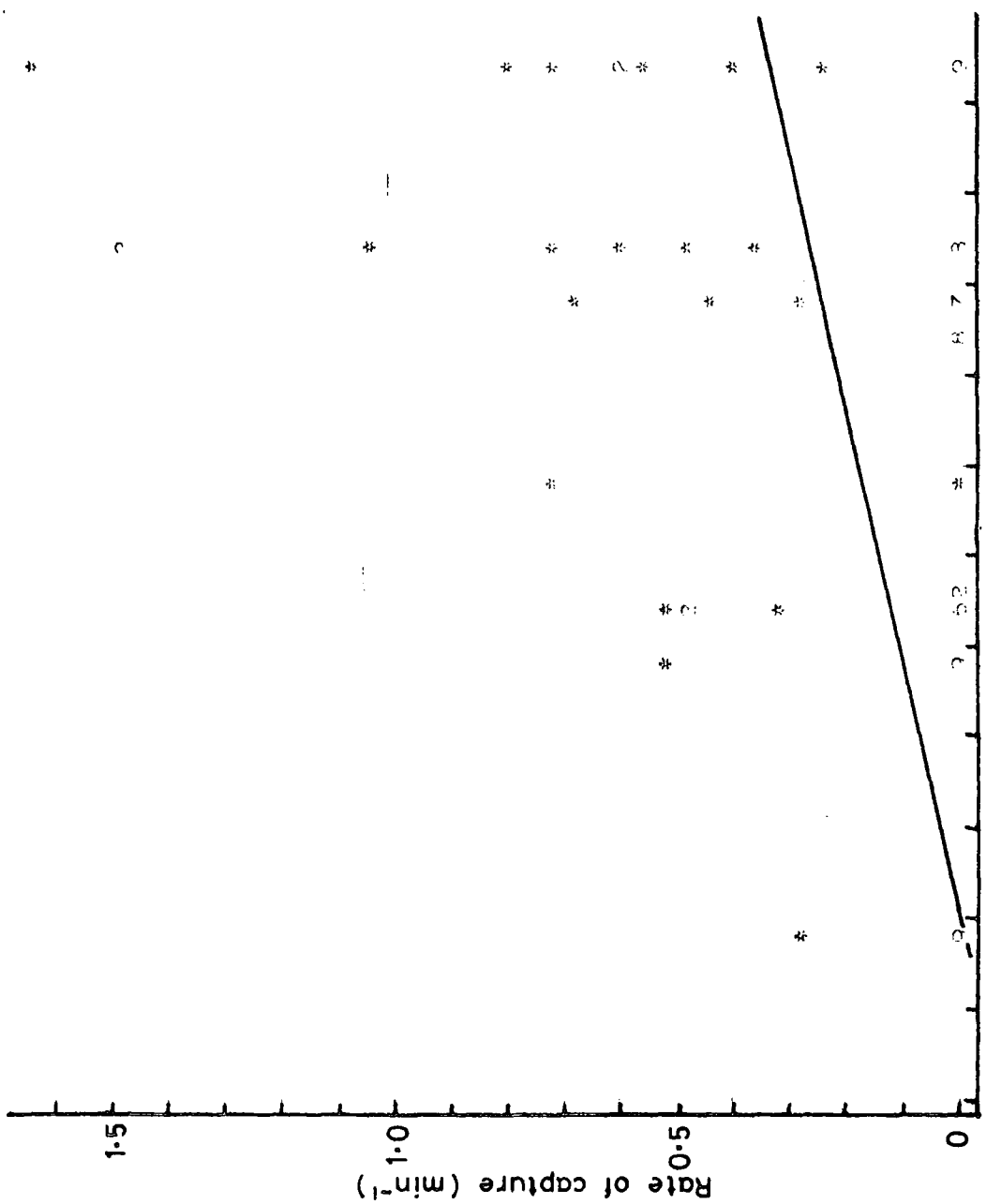


Figure 10. Rate of capture of *Arenicola* by Grey Plovers on the Low Flats in spring in relation to sand temperature.
Fitted regression line is $y = 0.03x - 0.094$ ($r = 0.30$, $P < 0.01$)

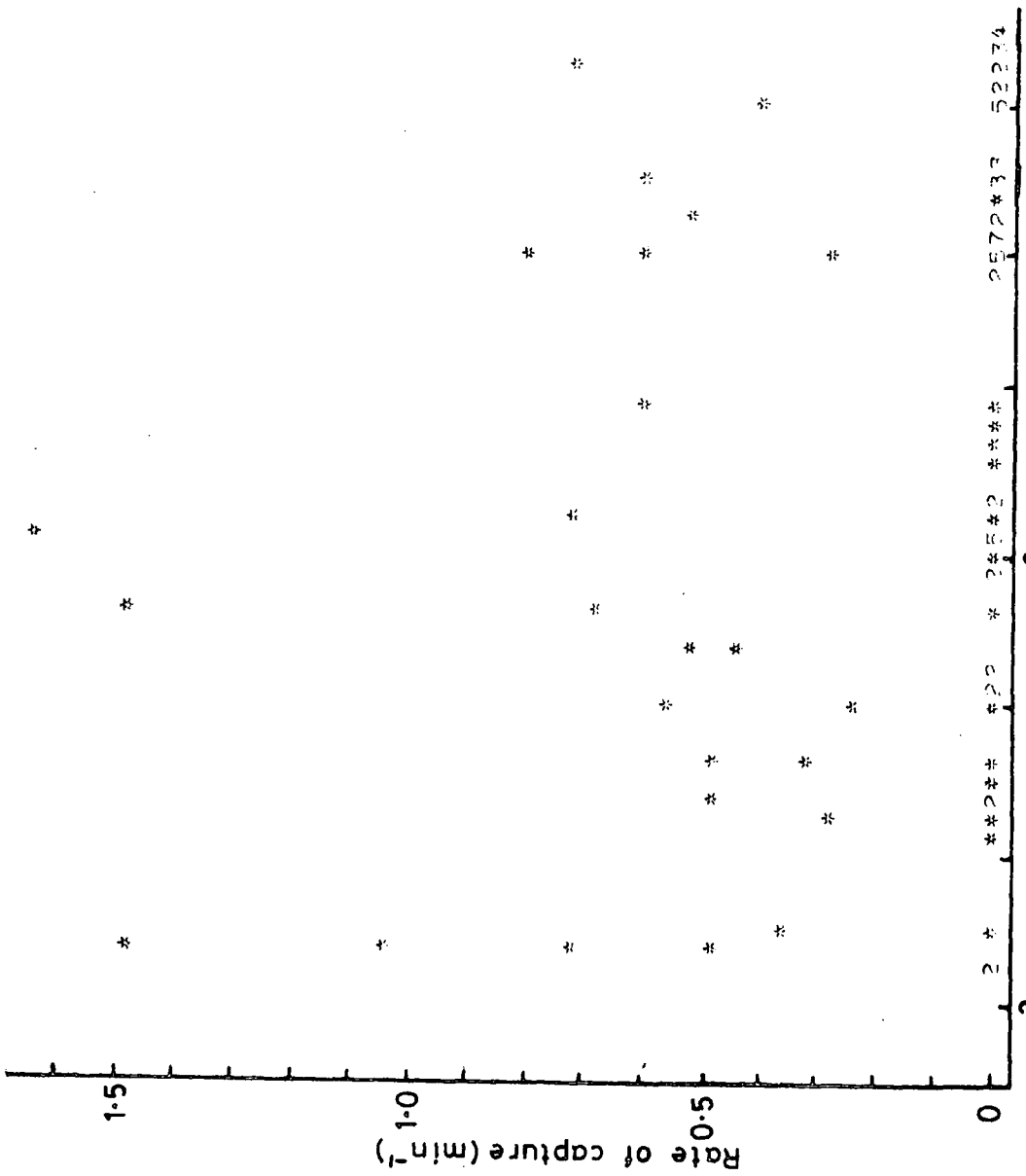


Figure 11. Rate of capture of *Arenicola* by Grey Plovers on the Low Flats in spring in relation to time after high water.

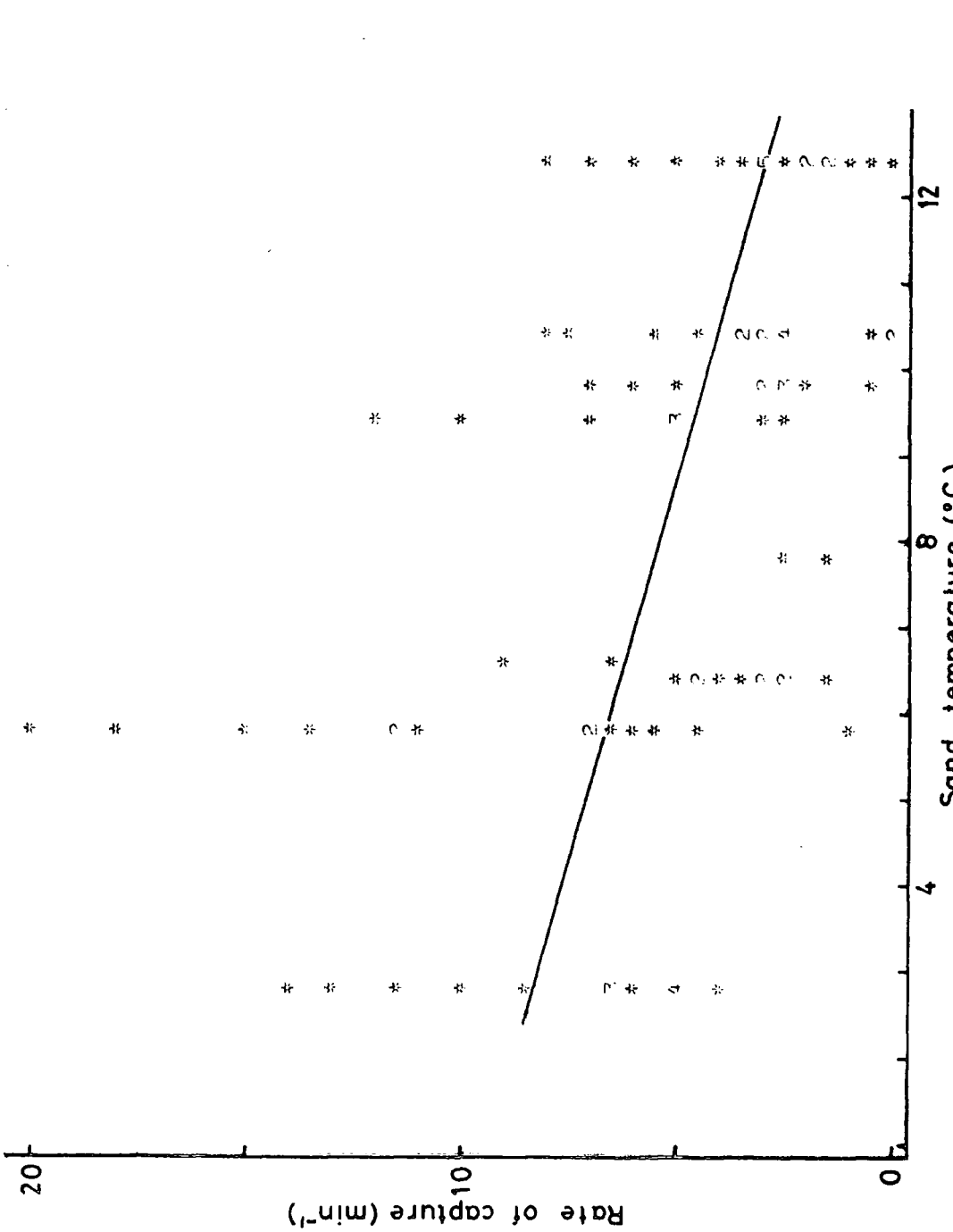


Figure 12. Estimated rate of capture of thin worms by Grey Plovers in spring on the Low Flats in relation to sand temperature.

Fitted regression line is $y = 10.03 - 0.59x$ ($r = 10.48$; $P < 0.001$).

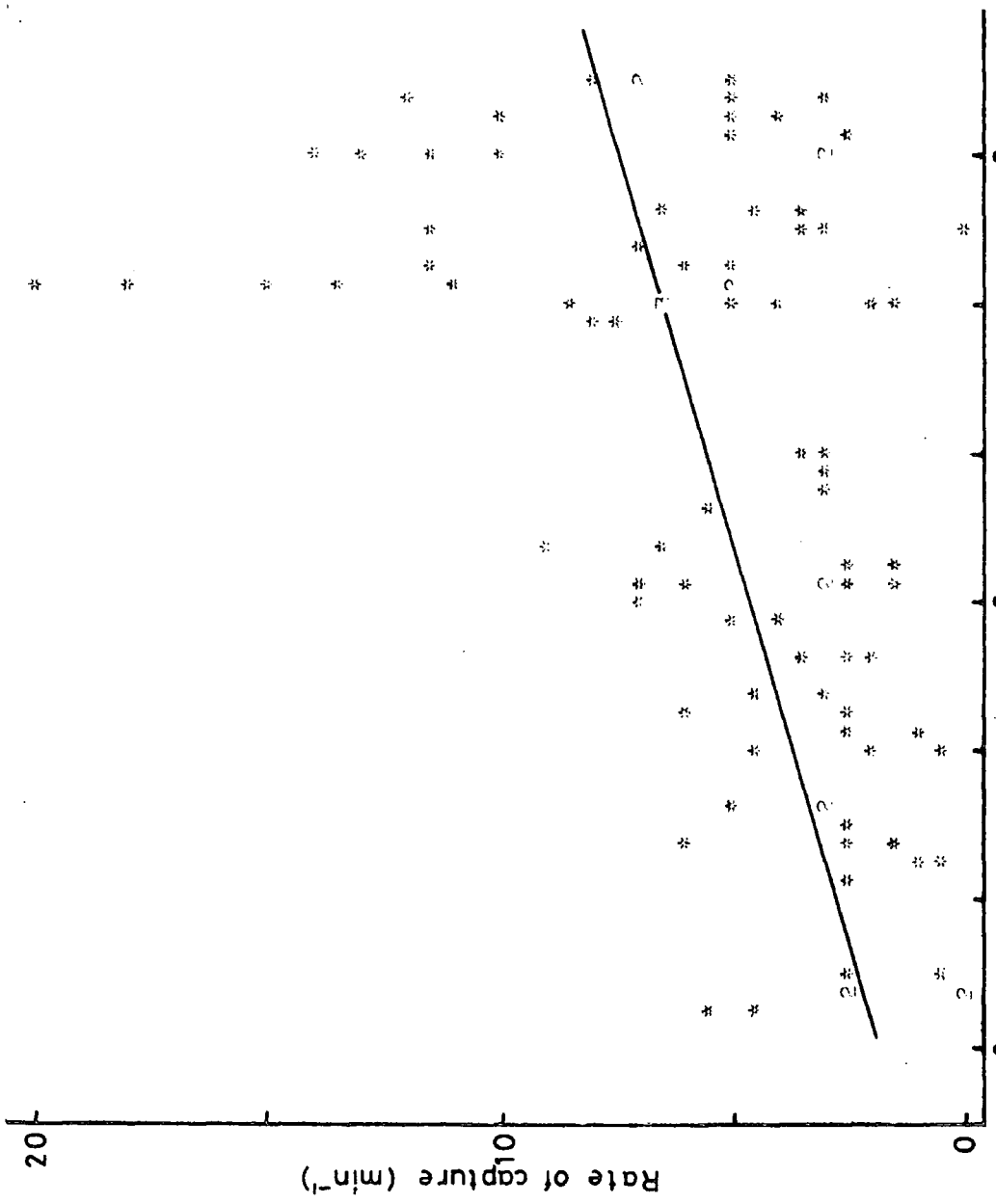


Figure 13. Estimated rate of capture of thin worms by Grey Plovers in spring on the Low Flats in relation to time after high water.

Fitted regression line is $y = 0.98x - 1.47$ ($r = 0.48$; $P < 0.001$)

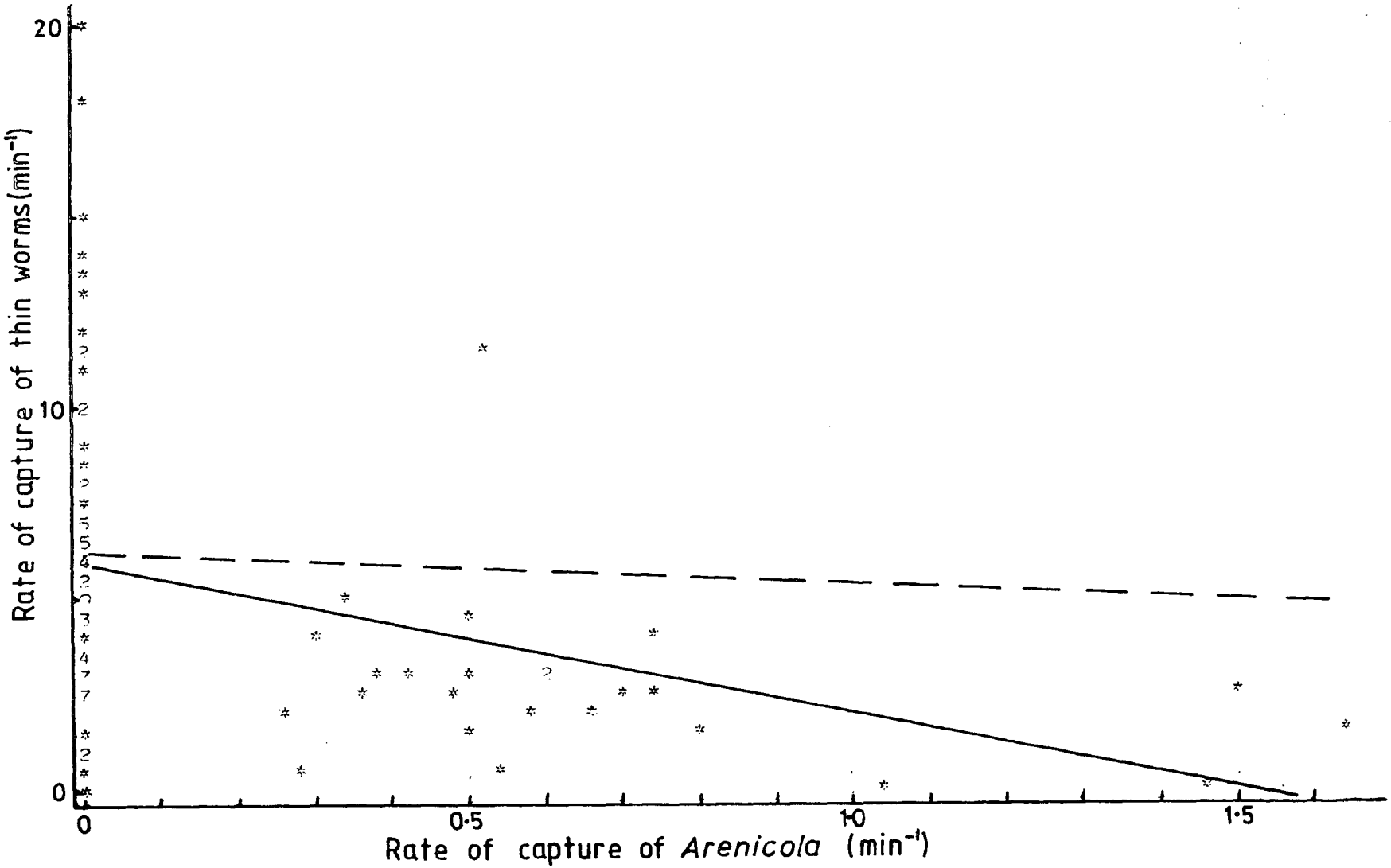


Figure 14. Estimated rate of capture of thin worms by Grey Plovers in spring on the Low Flats in relation to the rate of taking *Arenicola*.
Fitted regression line is $y = 5.93 - 4.12x$ ($r = -0.37$; $P < 0.001$)
Dashed line is expected slope if depression of rate of taking thin worms was solely due to reduction in foraging time because of time taken to handle *Arenicola*. This slope is significantly different from that of the regression ($t = 3.71$; $P < 0.001$).

similar relationship between rate of capture of thin worms and rain was suggested in many situations for both plovers but, because of the low number of occasions of observations during rain, it was significant in only this case).

In spring, the mean lengths of thin worms taken decreased with increases in temperature and the rate of capture of *Arenicola* but increased with increasing rainfall and time after high water (Table 4). In autumn and winter, the mean length of worms taken increased with time after high water.

Grey Plovers on the high tidal level flats

The diet of Grey Plovers on the High Flats was similar to that on the Low Flats (Paper 1). The rate of capture of *Arenicola* increased sharply from close to zero below 5.5°C (mean 0.02 ± s.e. 0.02 min^{-1}, n = 25) to a steady higher level above 5.5°C (mean 0.19 ± s.e. 0.04 min^{-1}, n = 91). This difference was highly significant (t_{114} = 4.07, P < 0.001) but there was no trend with temperature within each temperature group. The marked difference with season noted on the Low Flats did not occur on the High Flats, and the overall rate of capture of *Arenicola* was lower on the high level than on the low level flats during spring but higher at other times of year. Probably mainly because of low sample size, the rate of capture of *Arenicola* showed only one significant relationship with environmental factors, namely a decrease with increasing wind force at low temperatures.

Probably for similar reasons, the rate of capture of thin worms showed no significant relationship with environmental conditions at low temperatures, although the mean length of such worms appeared to increase with increasing wind and cloud cover. At higher temperatures, the rate of capture of thin worms increased with time after high water but decreased as the rate of capture of *Arenicola* increased. The mean rate of capture of thin worms declined from 4.61 ± s.e. 0.41 min^{-1} below 5.5°C to 3.15 ± s.e. 0.22 min^{-1} above (t_{114} = 3.19, P < 0.01). The detailed relationship of rate of capture of thin worms with mud temperature showed some similarity to that of Ringed Plovers, possibly increasing with temperatures up to about 5 - 6°C, followed by a decrease (Fig. 15). However, small sample sizes prevented this

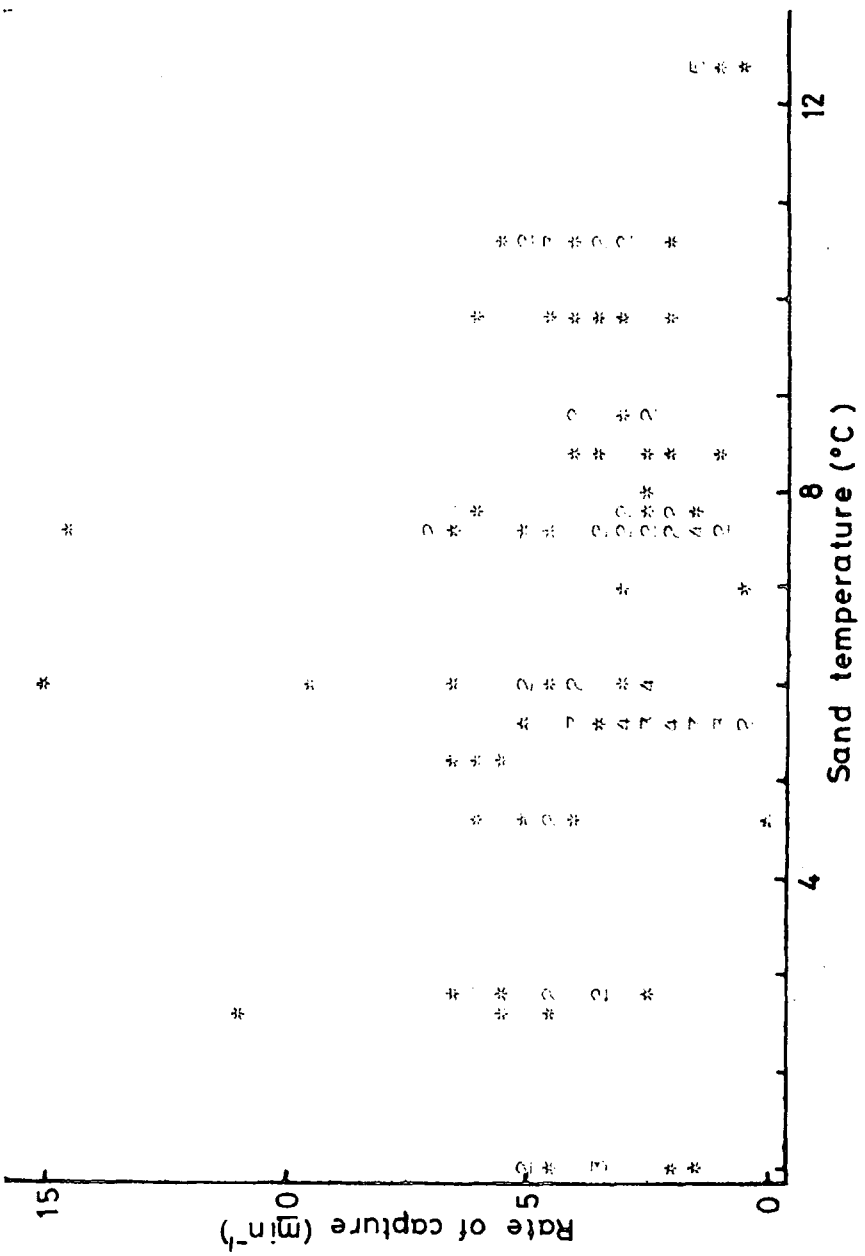


Figure 15. Estimated rate of capture of thin worms by Grey Plovers on the High Flats in relation to sand temperatures.

relationship from reaching statistical significance.

The mean length of thin worms taken decreased with increasing mud temperature but increased with increasing wind force, cloud cover and time after high water (Table 4).

EFFECTS OF OTHER BIRDS ON PREY CAPTURE RATES

Aggressive interactions between plovers feeding in flocks, or with birds of other species feeding nearby, were extremely rare, as also found for Grey Plovers at the Wash by Goss-Custard (1977b). Those few that were observed at Lindisfarne generally concerned Ringed Plovers as the breeding season approached. To investigate any other, more subtle, effects of birds on each other's feeding, distances to the nearest bird, to the nearest bird of the same species (which may be the same) and the number of birds of the same species in the flock were noted at the time of each feeding observation. Interpretation of any relationships found is more difficult than of those with environmental factors. If a significant correlation between the latter and prey capture rate is found, then there may or may not be a causal effect of the environmental factor on the rate. If a significant relationship between prey capture rate and flock-size or nearest neighbour distance is found, once again there may or may not be a causal link, but in these cases the possible causal links could be in either direction, e.g. of capture rate on flock size or *vice versa*. In contrast, a causal effect of rate of capture of worms on, e.g., windforce is highly unlikely! This ambiguity also causes difficulty in the use of multiple regression analyses involving these factors as well as environmental ones.

The relationships of rates of capture of various prey to flock-size and nearest neighbour distances are summarized in Table 7. When incorporated with environmental factors in multiple regression analyses the degree to which these relationships remained significant varied. 'Flock' factors occasionally displaced 'environmental' ones. However, the interpretation of this result is difficult, for reasons indicated above. Because the distance to the nearest other bird was often identical to the distance to the nearest other bird of the same species,

TABLE 7. RELATIONSHIPS BETWEEN FEEDING RATES AND FLOCK CONDITIONS

Arrangement as for Table 4.
(Distance of nearest bird of same species not included in multiple regressions. Multiple regressions include environmental variables as for Table 4).

	RINGED PLOVER				GREY PLOVER			
	Low Flats		High Flats		Low Flats		High Flats	
	<6 °C	⩾6 °C	<6 °C	⩾6 °C	autumn & winter	spring	<5.5°C	⩾5.5°C
Rate of taking thin worms								
Distance to nearest bird of same species	-0.17*	-	-0.30**	-0.40*	-0.20*	-0.23*	-	-
Distance to nearest bird (any species)	-0.18*	-	***-0.26**	-	-0.16*	-0.23*	-	-0.20*
Flock size	-	-0.40***	-0.29**	-0.56***	-	*** 0.60***	-	-0.21*
Rate of taking small prey					Rate of taking *Arenicola*			
Distance nearest same species	ne	ne	-0.25**	-0.30*	-	-	-	-
Distance nearest bird	ne	ne	***-0.21*	-	-	-	-	0.18*
Flock size	ne	ne	-0.28**	**-0.41**	-	-0.20*	-	-

simple correlations of capture rates with these two factors were very similar, and for this reason only the distance to the nearest bird was used in the multiple regressions analysis. A fairly consistent pattern emerged, however. With few exceptions the rate of prey capture decreased both with increasing flock-size and with increasing distance to the nearest other bird. Thus maximum feeding rates tended to occur in small, relatively tight flocks (or, conversely, flock-size increased and birds spread out when feeding rate dropped).

There was some evidence that plovers tended to occur in areas where densities of other shorebird species were low. This was difficult to test quantitatively because all species moved to some extent with the tides, thus leading to some degree of positive association. However, on 14 October 1974 the numbers of birds in several squares of side 100 m were counted during the low water period and the numbers of Ringed Plovers were inversely correlated with those of non-plovers ($r=-0.48$, $P<0.001$). However, on other occasions the relationship was not shown numerically as simply as this, because the plovers of both species merely kept away from the moving band of birds at the tide-edge and from any other areas where dense flocks of Bar-tailed Godwits and Dunlins tended to occur. Plovers very rarely fed in the water. An exception occurred, however, in spring (March to May inclusive) when Grey Plovers spread down to the tide edge and often fed in the water, particularly on the ebb tide. This period coincided with the absence of Bar-tailed Godwits from most of the area as most godwits leave Lindisfarne in March, whereas many Grey Plovers remain until May or early June.

HANDLING TIMES

The time taken to handle prey is defined as the time taken to move to the site from which the prey is taken, the time to handle it and the time until a waiting position is resumed. This parameter showed very little variation with environmental or flock conditions, although the handling times differed according to the prey taken (Table 8). Grey Plovers took significantly longer to handle *Arenicola* than thin worms and other small prey, and both plovers took longer to handle large thin red worms than small ones (Fig. 16). A similar

TABLE 8. HANDLING TIMES FOR CATCHING AND DEALING WITH PREY AND TIME TAKEN IN CHANGING WAITING POSITION

For the handling times, that including time to move to and/or from capture site (PLOVP2-type) is given above and that excluding the moving time and including only the time to peck and swallow prey (PLOVPROG-type) below. Given as mean ± s.e. (sample size). Within each site, statistically significant differences between handling times are indicated. In all cases (except one indicated) these apply to both types of data.

	RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats
Move without taking prey	0.68 ± 0.03 (163)	0.73 ± 0.05 (70)	1.14 ± 0.06 (115)	1.53 ± 0.06 (71)
Arenicola	31.3 ±27.3 (4)	2.16 ± 0.73 (5)	10.01 ± 2.72 (24)	12.04 ± 2.02 (31)
	31.1 ±27.4 (5)	1.91 ± 0.77 (5)	9.19 ± 2.76 (24) *	11.47 ± 2.06 (31) ***
Thin worms	1.71 ± 0.11 (222)	0.62 ± 0.16 (28)	2.23 ± 0.13 (153)	0.91 ± 0.15 (79)
	1.52 ± 0.10 (222) ***	0.52 ± 0.14 (28)	* 1.83 ± 0.12 (153) ***	*** 0.71 ± 0.12 (79) ** ns
Small items	0.93 ± 0.03 (196)	0.70 ± 0.04 (71)	1.48 ± 0.66 (132)	1.83 ± 0.19 (89)
	0.49 ± 0.02 (196)	0.42 ± 0.03 (71)	0.74 ± 0.05 (132)	0.87 ± 0.06 (89)

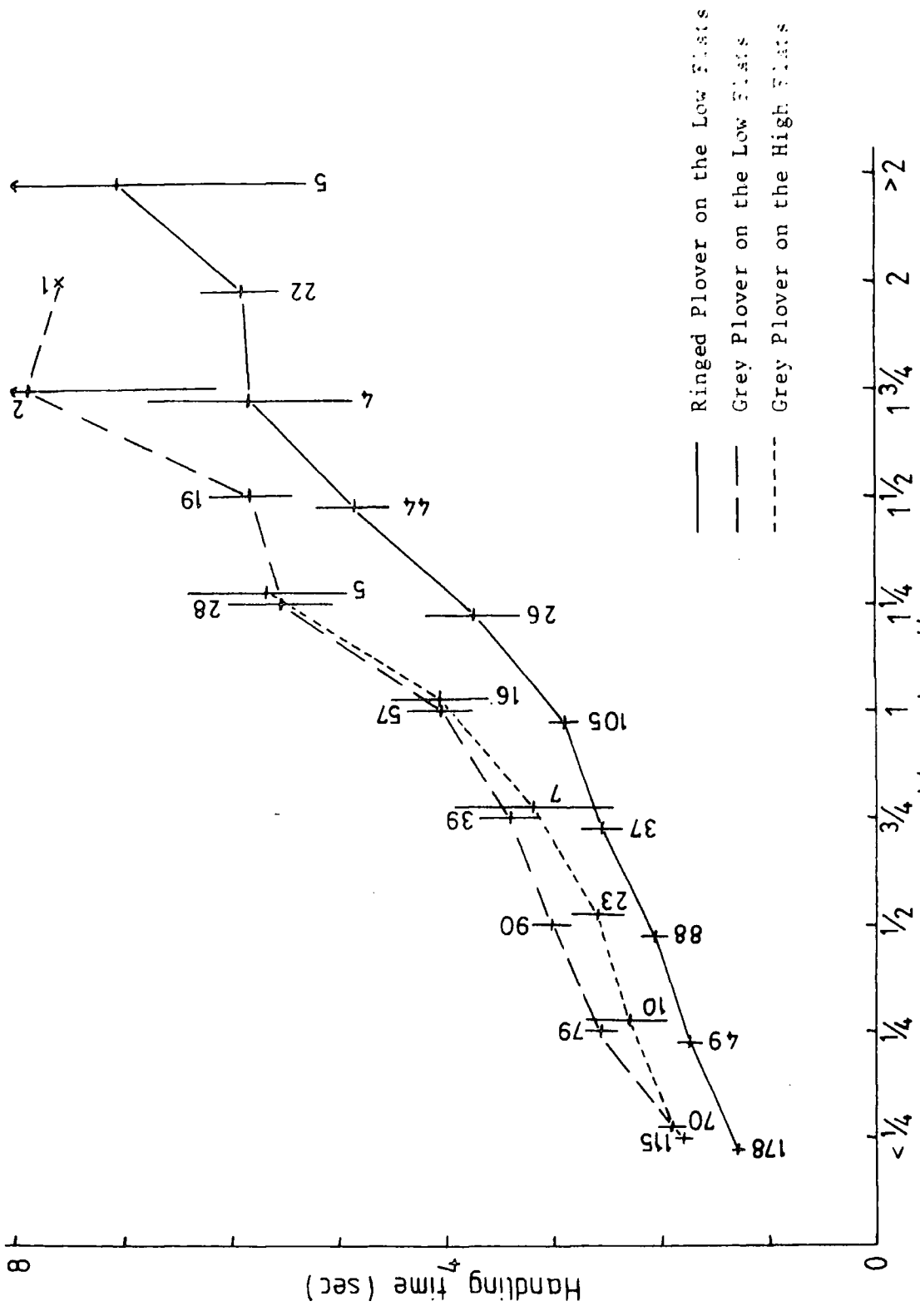


Figure 16. Handling times for thin worms of various sizes. Times, given as mean ± 1 standard error, with sample size noted. Worm lengths are measured relative to the height of a plover's bill off the ground (approximately 80 mm for Ringed Plovers; 120 mm for Grey Plovers).

increase in handling time with prey size was found for Great Blue Heron *Ardea herodius* by Krebs (1974). On the Low Flats plovers took less time to handle small items than worms but on the High Flats the times were fairly similar, probably bacause the worms taken there were mainly small.

On the Low Flats, the handling time for thin worms by Ringed Plovers increased significantly with rising temperature ($r_{168} = 0.29$, $P < 0.001$). This may have arisen because larger worms were taken in warmer conditions or because birds tended to wash worms more often before swallowing them in warmer weather (or for both reasons). Similarly, and for similar possible reasons, Grey Plovers took longer to handle *Arenicola* on the High Flats in warmer weather ($r_{25} = 0.37$, $P < 0.05$). However, in the same area, they took less time to handle thin worms ($r_{56} = -0.36$, $P < 0.01$) and small prey ($r_{60} = -0.28$, $P < 0.05$) with increasing temperatures, perhaps because the size of thin worms taken fell with increasing temperature. On the Low Flats the handling time of thin worms by Grey Plover increased with increasing windforce ($r_{151} = 0.17$, $P < 0.05$), perhaps because the birds experienced increasing difficulty in making directed movements in strong winds.

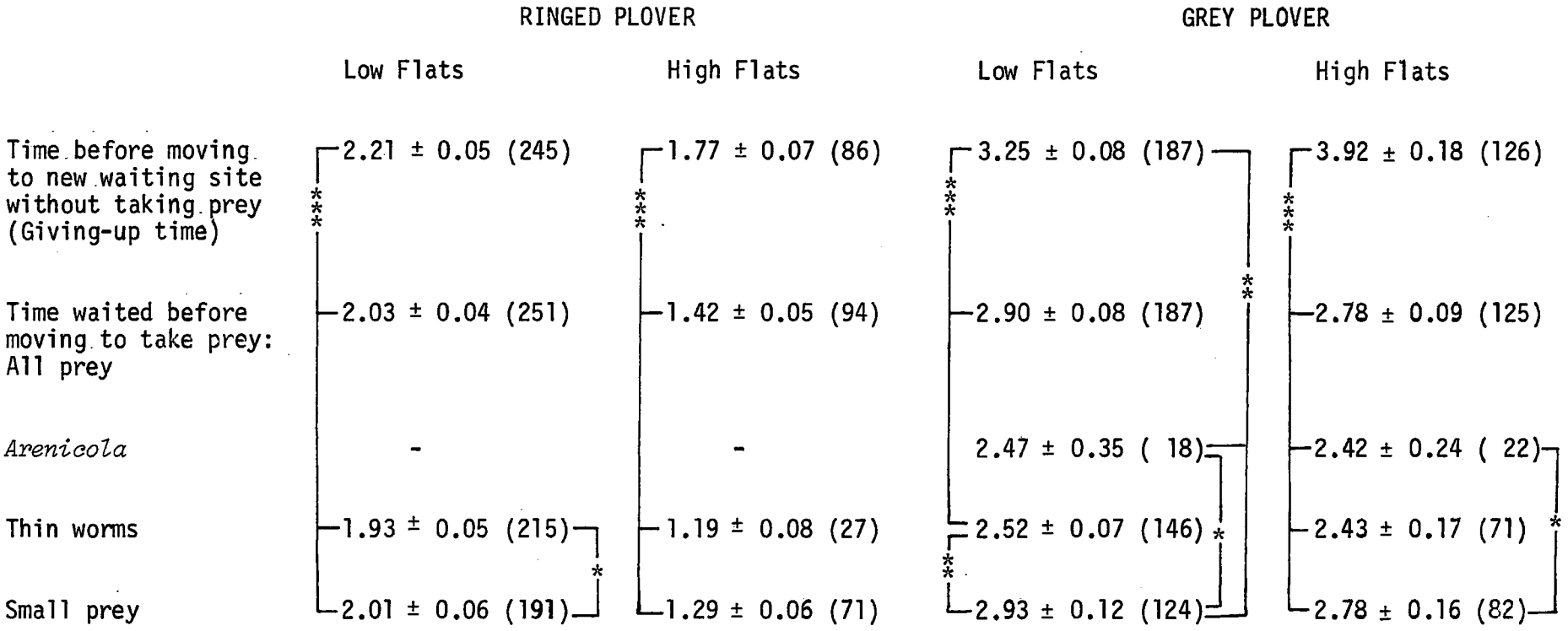
The mean handling times excluding the times taken to run to and from the capture sites (i.e. PLOVPROG-data, as defined in 'Methods') are also shown in Table 8. These data showed similar relationships with environmental conditions to those found for the 'PLOVP2-type' data.

WAITING AND GIVING-UP TIMES

The times spent in the 'up' position before moving to a new 'up' position (the 'giving-up' times) and the times spent in the 'up' position before moving to peck at prey (the 'waiting' times) are summarized in Table 9. Although waiting and giving-up times for any given site tended to be fairly similar, a consistent pattern can be discerned. Times increased through the series: waiting time before taking *Arenicola*, waiting time before taking thin worms, waiting time before taking small prey, giving-up time. Krebs (1974), studying Great Blue Herons, also found significantly longer giving-up times than waiting times.

TABLE 9. MEAN WAITING AND GIVING-UP TIMES

Statistically significant differences between giving-up times and any waiting times are indicated as are statistically significant differences between the three prey categories. *Sample sizes in parentheses.*



Giving-up times tended to be correlated with the waiting times (Table 10).

The relationships of waiting and giving-up times to environmental and flock conditions are summarized in Table 11. For both species on both High and Low Flats, patterns of giving-up and waiting times tended to be similar, probably even more so than indicated in Table 11, as small sample sizes prevented statistical significance in several cases. Also, several relationships that were significant in simple regression were not so in multiple regression, because the sample size was generally much reduced then.

For Ringed Plovers in both areas, both waiting and giving-up times appeared to lessen with rising temperature up to about $6^{o}C$ and then remain constant or increase above that (e.g. Fig. 17). Increases in wind force generally acted on timings in the opposite way to increases in mud temperature (Table 11). Other fairly consistent relationships were increases in times with increasing rainfall, increasing time after high water, distance to other birds and flock size (Table 11).

For Grey Plovers, waiting and giving-up times tended to increase with increases in the rate of capture of *Arenicola*, in mud temperatures and in wind force and to decrease with passage of time after high water (Table 11).

For Ringed Plovers in both areas the incidence of 'downs' increased with increasing temperature, increasing flock-size or decreasing wind force (Table 12). On the Low Flats the incidence of 'downs' also increased with time after high water and decreasing distance to the nearest other Ringed Plover. In Grey Plover, there was less consistency in the incidence of 'downs' between areas, but those relationships which were significant paralleled those for Ringed Plover, with the addition of an inverse relationship between incidence of 'downs' and the rate of capture of *Arenicola* on the High Flats. The capture of an *Arenicola* was significantly more likely to be preceded by an 'up' (rather than a 'down') than was the taking of a thin worm ($\chi^2_1 = 4.76$, $P < 0.05$).

TABLE 10. CORRELATION COEFFICIENTS AND THEIR SIGNIFICANCE LEVELS BETWEEN WAITING AND GIVING-UP TIMES

	RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats
Giving-up time with waiting times before taking:				
Any prey	0.47***	0.68***	0.48***	0.41***
Arenicola	-	-	0.29	0.22
Thin worms	0.33***	0.02	0.29***	0.19
Small prey	0.39***	0.49***	0.39***	0.56***

TABLE 11. RELATIONSHIPS BETWEEN WAITING AND GIVING-UP TIMES AND ENVIRONMENTAL AND FLOCK CONDITIONS

Arrangement as for Tables 4 & 7.

	RINGED PLOVER				GREY PLOVER	
	Low Flats		High Flats		Low Flats	High Flats
	<6 °C	≥6 °C	<6 °C	≥6 °C		
Giving-up time						
Rate of taking *Arenicola*	***-0.18	-	* 0.24	-	* 0.18***	0.15*
Mud temperature	*-0.27*	-	***-0.73***	-	-	0.22*
Wind force	0.14*	-	*** 0.70***	-	0.14*	-
Rain[1]	-	-	-	-	-	-
Cloud	-0.19*	-	-	-	-	-
Time after HW	* 0.13	-	0.33**	* 0.38*	*-0.24***	-
Distance to nearest same sp.	-	-	0.53***	-	-	-
Distance to nearest bird[1]	-	-	0.54***	-	-	-
Flock size	-	-	* 0.56***	-	-	0.17*
Waiting time						
Rate of taking *Arenicola*	-	-	-	* 0.24	-	0.33***
Mud temperature	***-0.13	* 0.20	-0.52***	-	-	* 0.39***
Wind force	-	-	*** 0.55***	-	* 0.21*	-
Rain[1]	0.25***	-	-	0.30*	-	-0.17*
Cloud	-	-	-	-	-	-
Time after HW	*** 0.29**	* 0.24	0.38**	-	*-0.18**	-
Distance to nearest same sp.	* 0.19*	-	-	-	-	-
Distance to nearest bird[1]	0.19*	-	-	-	-	-
Flock size	-	-	0.35**	-	-	-

[1] excluded from multiple regression

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

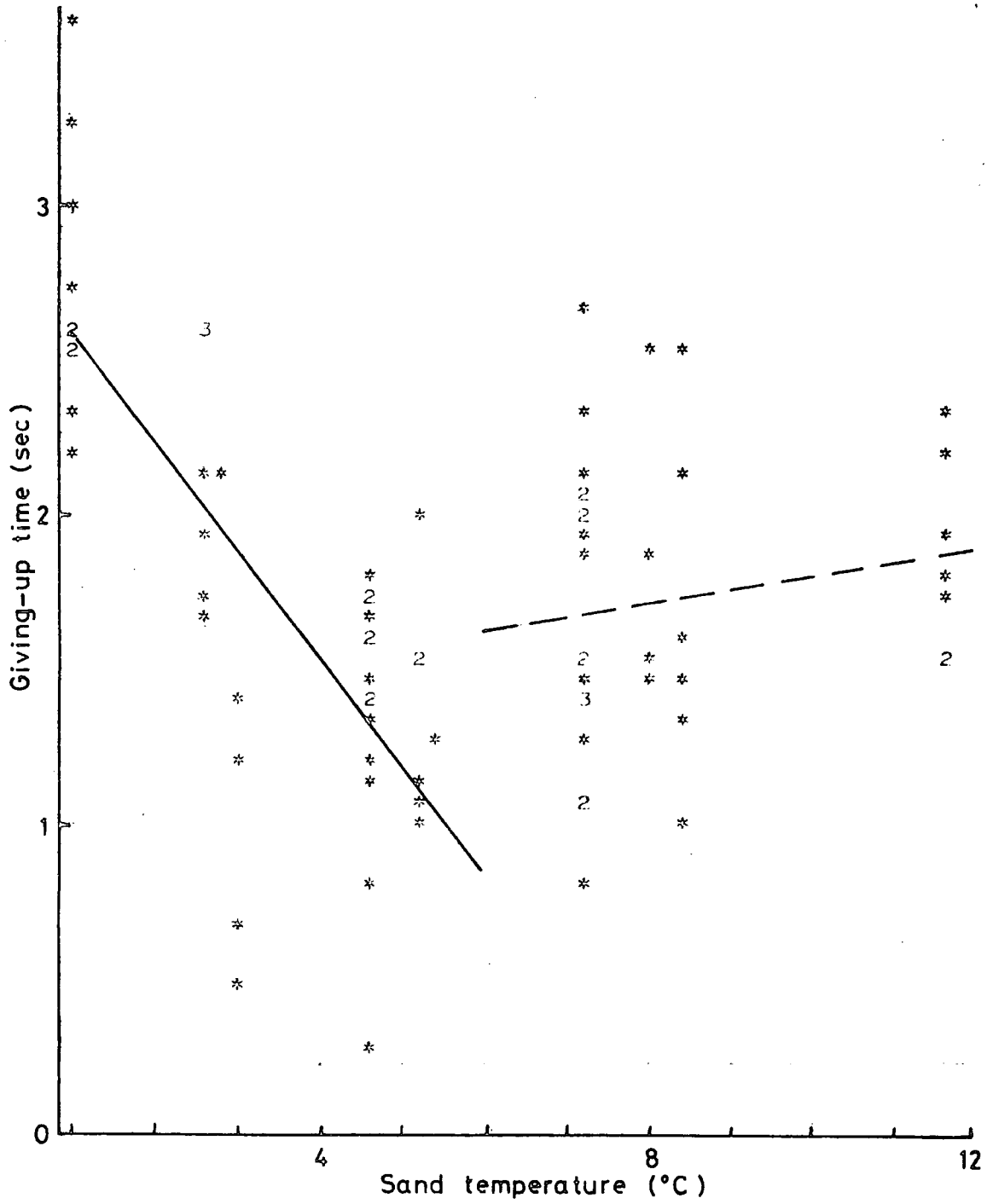


Figure 17. Giving-up timé (time spent in 'up' before moving on without taking prey) of Ringed Plovers on the High Flats in relation to sand temperature.

Fitted regression lines are: $y = 2.91 - 0.34x$ ($P < 0.001$) below $6^{o}C$
and $y = 1.40 + 0.04x$ (n.s.) above $6^{o}C$

TABLE 12. RELATIONSHIPS BETWEEN RATE OF OCCURRENCE OF 'DOWNS' AND ENVIRONMENTAL AND FLOCK CONDITIONS

Arrangements as for Table 11.

	RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats
Rate of taking *Arenicola*	-	-	-	*-0.17*
Mud temperature	** 0.44**	* 0.30*	-	-
Wind force	-0.26**	**-0.32**	**-0.17*	-
Rain[1]	-	-	-	-0.15*
Cloud	-	-	-	-
Time after high water	0.15*	-	** 0.32**	-
Distance to nearest same sp.	-0.12*	-	-	-
Distance nearest bird[1]	-	-	-0.18*	-
Flock size	0.33**	** 0.52**	0.12*	-

DISTANCES MOVED WHILE FORAGING, AND SEARCH AREAS

The distances birds moved to take prey did not differ significantly with prey type (Table 13) but this may have been partly due to low sample sizes. In all cases the mean distance moved to take prey was significantly less than the mean distance moved to a new 'up' position. The mean distance moved to a 'down' position was intermediate.

Distances moved varied relatively little with environmental and flock conditions (Table 14). General tendencies were an increase in distances moved (both to take prey and to a new 'up' position) with increasing distance to the nearest other bird of the same species; also a tendency for a decrease with increasing temperature, except for Grey Plovers on the Low Flats where the distances they moved increased with the rate of capture of *Arenicola*.

The distance moved to a new waiting position varied according to the previous activity (Table 15). Birds moved farthest between two 'up' positions and less far (in decreasing sequence) after taking pecks of unknown outcome, small prey, thin worms of increasing size and the least distance after taking *Arenicola*.

The frequency distributions of distances moved to a new position and particularly the distances moved to take prey tended to show fairly sharp upper limits (Table 16). These upper limits are estimated in Table 16. As birds can take prey within about $\frac{1}{2}$ pace (c5 cm for Ringed Plover; c7 cm for Grey Plover) without moving another pace, it can be seen that the average distance moved to a new waiting position (Tables 13, 15) tended to be slightly longer than the normal range from waiting position to the site of prey capture.

For estimation of the distance through which birds move in an attempt to take prey (Table 17) the 'normal' maximum number of paces taken to reach prey has been increased by one to allow for both the distance at which a bird can reach prey without taking another pace and the slight bias towards underestimation of the recording methods (see 'Methods').

TABLE 13. MEAN NUMBERS OF PACES MOVED TO TAKE UP NEW WAITING POSITION OR TO TAKE PREY

Statistically significant differences between movements to various prey types and between these or total pecks and movements to new waiting positions are indicated.

	RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats
No. of paces to:				
Up	3.99 ± 0.26 (45)	5.26 ± 0.62 (30)	5.42 ± 0.43 (56)	7.82 ± 0.46 (37)
Down	3.38 ± 0.64 (7)	3.75 ± 0.48 (4)	3.68 ± 0.20 (33)	4.55 ± 0.60 (18)
Peck (any outcome)	2.01 ± 0.13 (45)	1.76 ± 0.14 (31)	2.04 ± 0.20 (56)	2.32 ± 0.24 (37)
Peck - *Arenicola* taken	(0)	3.00 (1)	3.75 ± 2.13 (10)	2.00 ± 0.71 (4)
Peck - thin worm taken	2.15 ± 0.26 (38)	2.11 ± 0.53 (7)	2.25 ± 0.26 (41)	2.74 ± 0.73 (12)
Peck - small prey taken	2.72 ± 0.42 (28)	1.71 ± 0.48 (12)	2.15 ± 0.20 (32)	3.22 ± 0.34 (22)

TABLE 14. RELATIONSHIPS OF DISTANCES MOVED TO NEW WAITING POSITION AND TO TAKE PREY WITH ENVIRONMENTAL AND FLOCK CONDITIONS

Arrangement as for Table 11.

	Movement to new 'up' position				Movement to peck			
	RINGED PLOVER		GREY PLOVER		RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats	Low Flats	High Flats	Low Flats	High Flats
Mud temperature	-	-0.58***	* 0.40*	-0.45*	-0.26*	-	-	-
Wind	-	0.51*	-	-0.30*	-	-	-	-
Rain	-	-	-	-	-	-	-	-
Cloud	-	-	-	-	* 0.27*	-	-	-
Tide	-	*** 0.50*	-0.41**	-	-0.27*	-	-	-
Distance nearest same sp.	* 0.32*	0.60**	-	-	-	-	-	0.40*
Distance nearest bird	0.38*	-	-	-	-	-	-	0.33*
Flock size	-	0.58**	*-0.28*	-	-0.27*	-	-	-
Rate of taking *Arenicola*	nd	-	*** 0.57**	-	nd	-	* 0.43**	-

TABLE 15. MEAN NUMBERS OF PACES MOVED TO A WAITING POSITION IN RELATION TO PREVIOUS ACTIVITY OR PREY

Given as mean ± s.e. (sample size). Statistically significant differences are indicated.

	RINGED PLOVER		GREY PLOVER	
	Low Flats	High Flats	Low Flats	High Flats
No. of paces moved to waiting position after:				
Up (no prey taken)	4.89 ± 0.46 (35)	6.16 ± 0.66 (24)	6.39 ± 0.46 (45)	9.26 ± 0.57 (29)
Peck (unknown outcome)	2.60 ± 0.40 (35)	1.12 ± 0.25 (24)	2.91 ± 0.42 (45)	3.67 ± 0.85 (29)
Peck: Small prey taken	1.52 ± 0.36 (29)	1.50 ± 0.98 (12)	2.17 ± 0.37 (32)	2.82 ± 0.78 (24)
Peck: *Arenicola* taken	(0)	0.00 (1)	0.00 ± 0.00 (9)	0.00 ± 0.00 (4)
Peck: Thin worm ≤ ¼ x bill-height taken	1.35 ± 0.23 (26)	0.20 ± 0.20 (5)	2.76 ± 0.81 (35)	2.24 ± 0.85 (15)
Peck: Thin worm ½ to 1 x bill-height taken	1.22 ± 0.29 (17)	0.00 ± 0.00 (3)	1.63 ± 0.33 (33)	0.67 ± 0.67 (3)
Peck: Thin worm > bill-height taken	8.80 ± 7.81 (5)	(0)	1.17 ± 0.54 (6)	(0)

TABLE 16. AVERAGE DISTANCES (NO. OF PACES) MOVED TO TAKE PREY AND TO NEW POSITIONS IN EACH CASE

'Normal' maxima (see text) are given.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	'Normal limit'	% within this limit
Ringed Plover Low Flats																								
To 'up'	0	0	11	16	2	7	5	3	0	1													7	98
To 'down'	1	0	0	1	3	2																	5	100
To take prey	0	16	20	7	0	2																	3	96
Ringed Plover High Flats																								
To 'up'	0	0	3	9	7	1	2	1	2	0	2	2	0	0	0	1							-	-
To 'down'	0	0	0	1	1	1																	5	100
To take prey	1	15	12	1	2																		4	100
Grey Plover Low Flats																								
To 'up'	0	0	4	11	16	6	3	5	3	3	2	2	0	0	0	0	0	0	0	0	0	1	11	98
To 'down'	0	1	3	9	12	4	4																5	100
To take prey	4	19	24	7	1	0	0	0	0	0	0	1											4	98
Grey Plover High Flats																								
To 'up'	0	0	0	0	2	4	6	9	4	3	3	0	2	2	2								13	100
To 'down'	1	1	2	3	1	5	3	0	0	1	1												6	89
To take prey	1	9	15	4	6	0	1	1															4	95

TABLE 17. ESTIMATION OF SEARCH AREAS (see text)

	RINGED PLOVER	GREY PLOVER
Pace length (cm)	10	14
'Normal' maximum no. of paces moved to prey	3	4
'Normal' maximum foraging radius	4 x 10 = 40 cm	5 x 14 = 70 cm
'Normal' arc of movement	240^{o}	240^{o}
Search area = $\frac{240}{360} \pi r^2$	0.34 m^2	1.03 m^2

The mean length of paces was estimated from ciné-film and from measurement of tracks on the flats. The angle turned from the waiting position to the direction chosen when moving to take prey was estimated on a 'clock' basis from examination of ciné-film (Fig. 18). These measures are combined in Table 17 to estimate the search area from which prey can be taken.

The foraging method of a plover, which uses a search area of fairly constant size with a changeable location, is compared in Figure 19 with that of a sandpiper foraging by touch with bill-tip on the surface or inserted slightly into the substratum. The latter uses a narrow search area determined by detection distance on either side of the path taken (see, e.g., Smith 1975, Hulscher 1976). The sandpiper search area is thus an area searched per unit time. In contrast, plovers are generally sit-and-wait predators, monitoring an area until a suitable prey is detected, or until the bird gives up to move to a new waiting position.

FOOT VIBRATION

Foot-vibration while foraging has often been reported in plovers (e.g. Simmons 1961). In this behaviour, the bird stands on one leg with the toes of the other just in contact with the ground and vibrating rapidly. At Lindisfarne, this was recorded on only one occasion in Grey Plovers: a bird feeding in November near the small salt-marsh, an area not much used by this species.

However, foot-vibration by Ringed Plovers was recorded commonly on the highest intertidal areas: near the small salt-marsh, the North Shore, the Sand Rig and Goswick Flats, but infrequently on the main areas of the flats (Table 18). On none of the high level areas was a significant difference found in pecking rate between birds foot-vibrating and those not (Table 19). However, when the environmental conditions during cases when foot-vibration was seen are compared with those during cases without (Table 20), footshaking occurred at significantly lower mean temperatures on the North Shore. The same relationship was found on the High Flats near the Rig, but this was not significant, probably due to small sample size. A significant temperature difference

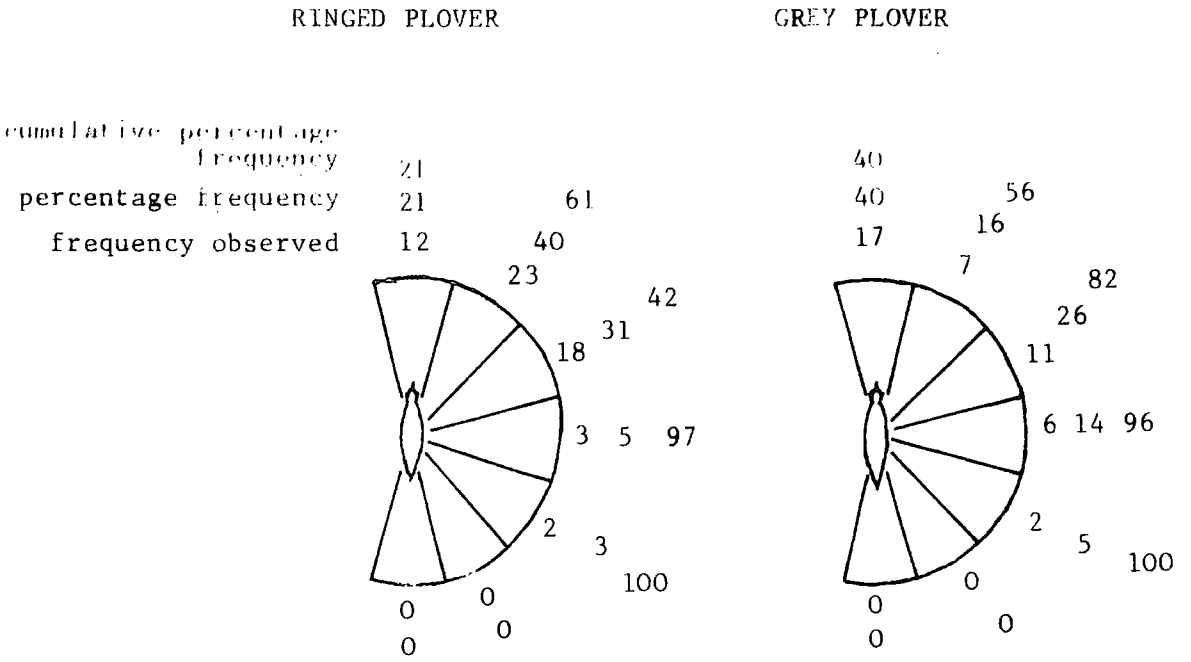


Figure 18. Directions moved to take prey.

Turns to left or to right through the same angle are not separated

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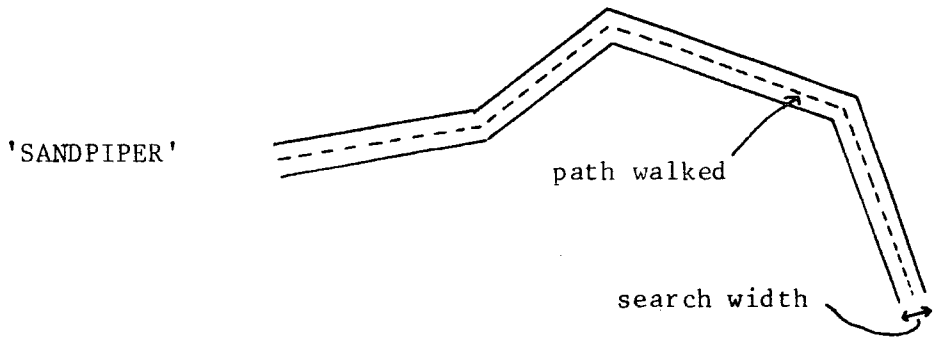
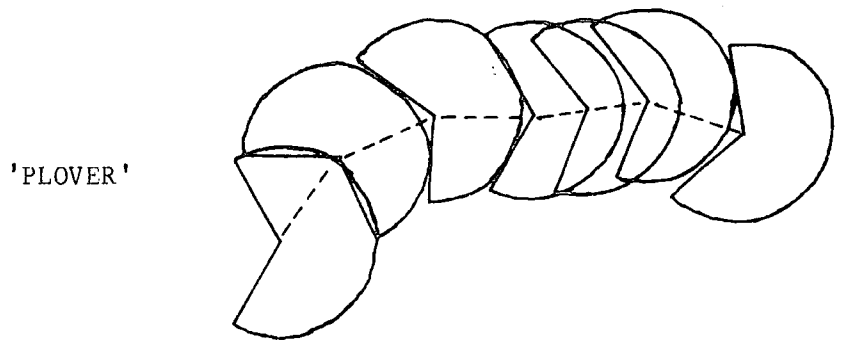


area searched per unit time = distance moved in unit time x search path width



search area = approximately constant area with changeable location

Figure 19. Generalized foraging patterns of tactile feeding sandpiper and visual searching plover.

TABLE 18. OCCURRENCE OF FOOT-VIBRATION IN FULLY-GROWN RINGED PLOVERS IN RELATION TO LOCATION AND MONTH

Upper line is number of cases where foot-vibration was not shown and the lower line those cases in which foot-vibration occurred for some or all the time.

Overall 103/574 (18%) of cases involved foot-vibration.

Month	J	J	A	S	O	N	D	J	F	M	A	M
North Shore	9	31	44	2	-	-	-	-	4	10	41	11
	0	3	0	0	-	-	-	-	-	9	18	6
Rig											8	
											16	
Near Causeway bridge			13									
			0									
Near small salt marsh	-	-	3	9	3	3	-	24	1	6	2	-
	-	-	0	0	6	0	-	10	3	0	15	-
Elsewhere on High Flats						4						
						0						
Low Flats	-	-	23	35	21	8	5	44	7	44	-	-
	-	-	0	0	5	0	0	1	0	1	-	-
Holy Island Harbour								2				
								0				
Tealhole	6											
	8											
Inner Old Law		12	15									
		1	0									
Guile Pt. - Ross Back Sands		4	17									
		0	0									

TABLE 19. MEAN RATES OF PECKING BY RINGED PLOVERS IN SELECTED SITES AND MONTHS IN RELATION TO FOOT-VIBRATION

Given as mean ± s.e. (sample size)

		Birds foot-vibrating for some or all time		Birds not foot-vibrating
North Shore and Rig	April	19.4 ± 1.3 (37)	ns	19.7 ± 1.8 (43)
Near small salt marsh	April	24.3 ± 2.0 (15)	ns	25.8 ± 3.6 (2)
Tealhole	June	16.6 ± 3.0 (8)	ns	17.1 ± 2.9 (6)

TABLE 20. MEAN ENVIRONMENTAL CONDITIONS DURING OBSERVATION CASES OF RINGED PLOVERS IN RELATION TO FOOT-VIBRATION

	Birds foot-vibrating for some or all time		Birds not foot-vibrating
North Shore			
Air temperature	10.4 ± 0.8 (32)	***	14.7 ± 0.4 (141)
High Flats near Rig			
Air temperature	11.2 ± 1.1 (20)	ns	15.5 ± 4.9 (4)
High Flats near small salt marsh			
Air temperature	5.3 ± 0.2 (34)	ns	5.7 ± 0.7 (40)
Wind force	4.8 ± 0.5 (34)	*	3.7 ± 0.3 (52)
Rain fall	0.9 ± 0.3 (34)	*	0.2 ± 0.1 (52)

between cases with and without foot-vibration was not found on the High Flats near the small salt marsh, but the behaviour there was associated with stronger winds and heavier rain.

NOCTURNAL FORAGING

Observation on foraging behaviour of Grey Plovers were made with a night-viewing apparatus on Holy Island Sands on a dark, moonless night in February 1976 and a moon-lit night in March 1976. The results are compared with those from daylight feeding in the same weather conditions in Table 21 (see also Paper 1). At night the Grey Plovers fed in more discrete, tighter and more synchronised flocks than during the day but this was not quantified.

Pecking rates on the dark night, but not on the moon-lit night, were significantly lower than in daylight. The sequence 'run-peck' was more frequent by day than by night in both situations and the mean distance moved to take prey was longer in daylight. In March, the sequence 'up-peck' was significantly more frequent by night. Waiting times tended to be longer at night.

Nocturnal observations on foraging behaviour of Ringed Plovers were possible only when the birds could be observed at close quarters, on the breeding grounds of the North Shore. For both adults and chicks, differences between foraging by day and night (Table 22) were fairly similar to those found for the Grey Plovers, but, because of small sample sizes, fewer relationships were statistically significant.

DISCUSSION

A model of plover foraging

The results described in this paper allow me to put forward a model to describe the foraging behaviour of plovers. Taking the Grey Plover at Lindisfarne as as example, these tentative rules are:

1. Grey Plovers feed in areas where their rate of energy intake is high.
2. This may be modified in that plovers do not feed in areas of high density of other birds, which for Grey Plovers at Lindisfarne

TABLE 21. NOCTURNAL FORAGING BEHAVIOUR OF GREY PLOVERS ON HOLY ISLAND SANDS

	February 1976			March 1976		
	Day		Night	Day		Night
Pecking rate (min^{-1})	8.18 ± 0.65 (25)	***	4.15 ± 0.64 (18)	4.99 ± 0.49 (33)	ns	4.85 ± 0.73 (6)
Rate Up → peck (min^{-1})	5.80 ± 0.82 (25)	ns	4.48 ± 0.66 (18)	3.38 ± 0.52 (33)	*	6.45 ± 0.96 (6)
Rate Run → peck (min^{-1})	1.94 ± 0.66 (25)	*	0.37 ± 0.18 (18)	1.45 ± 0.39 (33)	***	0.00 ± 0.00 (6)
Rate Down (min^{-1})	0.90 ± 0.21 (25)	**	0.12 ± 0.08 (18)	0.91 ± 0.20 (33)	***	0.00 ± 0.00 (6)
Giving-up time (sec)	3.57 ± 0.31 (17)	ns	4.02 ± 0.87 (14)	4.32 ± 0.39 (19)	ns	3.76 ± 0.92 (4)
Waiting time (sec)	2.46 ± 0.17 (17)	ns	5.71 ± 1.74 (14)	2.80 ± 0.21 (18)	*	4.06 ± 0.63 (5)
Inter-wait run time (sec)	1.26 ± 0.13 (17)	ns	1.66 ± 0.28 (14)	1.45 ± 0.14 (19)	ns	1.30 ± 0.66 (5)
Inter-wait run distance (no. of paces)	6.86 ± 0.78 (8)	ns	10.55 ± 2.95 (4)	7.87 ± 0.81 (14)		4.75 (1)
Distance run to take prey (no. of paces)	2.78 ± 0.34 (8)	*	1.18 ± 0.30 (4)	2.64 ± 0.51 (13)		(0)

TABLE 22. NOCTURNAL FORAGING BEHAVIOUR OF RINGED PLOVERS ON NORTH SHORE

	Adults, June			Chicks, July		
	Day		Night	Day		Night
Pecking rate (min^{-1})	17.51 ± 1.54 (40)	***	7.24 ± 0.96 (6)	11.36 ± 1.20 (16)	ns	9.66 ± 1.55 (3)
Rate Up → Peck (min^{-1})	5.63 ± 1.36 (40)	ns	8.17 ± 0.84 (6)	6.81 ± 0.86 (16)	ns	9.16 ± 1.74 (3)
Rate Run → Peck (min^{-1})	0.96 ± 0.68 (40)	ns	0.00 ± 0.00 (6)	0.83 ± 0.61 (16)	ns	0.00 ± 0.00 (3)
Rate Down (min^{-1})	0.01 ± 0.01 (40)	ns	0.00 ± 0.00 (6)	1.24 ± 0.30 (16)	***	0.00 ± 0.00 (3)
Giving-up time (sec)	2.01 ± 0.18 (14)	ns	4.52 ± 1.48 (5)	1.63 ± 0.09 (14)	ns	2.10 ± 0.35 (3)
Waiting time (sec)	2.03 ± 0.24 (14)	***	3.85 ± 0.46 (6)	1.69 ± 0.21 (14)	ns	2.61 ± 0.48 (3)
Inter-wait run time (sec)	0.66 ± 0.09 (13)	*	1.23 ± 0.27 (5)	0.80 ± 0.22 (14)	ns	0.88 ± 0.21 (3)
Inter-wait run distance (no. of paces)	2.17 ± 0.47 (2)		(0)	4.13 ± 0.23 (2)		(0)
Distance run to take prey (no. of paces)	1.69 ± 0.23		(0)	2.85 ± 1.07 (2)		(0)

usually means flocks of Bar-tailed Godwits feeding at the tide edge where prey availability is highest.

3. As temperatures fall or the mud dries *Arenicola* become less available and smaller worms, notably *Notomastus*, are taken more frequently.
4. As temperatures fall, *Notomastus* also become less available, and less size selection is practised by the birds.
5. In the most adverse conditions the rate of taking thin worms of any size is depressed by reduced availability.
6. The plovers feed by scanning a search area. If prey are not detected the bird moves approximately far enough to see the next area beyond. When feeding on very dispersed clumps of prey, the bird may move further.
7. Most intertidal invertebrates tend to be distributed patchily, especially when availability as well as density is considered. Plovers adjust to this by moving less far after taking a prey than not. The distance moved appears to be adjusted to the value of the prey.
8. Plovers appear to adjust their giving-up time to the time they have to wait before taking prey; this is monitored fairly rapidly.
9. Prey selection appears to be achieved by becoming progressively more prepared to take smaller prey within each waiting period.
10. Plovers at Lindisfarne appear to feed as close to the other members of their flock as their feeding requirements (scan and run distances) allow. The inter-bird distance increases when reacting mainly to the widespread cues of *Arenicola*, but within a prey type decreases as prey activity increases, e.g. with rising temperatures. (In other situations, notably as Teesmouth, this relationship does not hold as the birds defend feeding territories - D.J. Townshend in Evans 1976.)
11. At night detection range was reduced and birds tended to pack more closely.
12. Plovers are well able to feed at night but probably less successfully in decreasing light. They appear to prefer to feed in daylight.
13. In adverse conditions, plovers tend to form larger flocks, probably on the best feeding areas.

A similar scheme could be written for Ringed Plovers, except that *Arenicola* is a less important prey and small Crustacea of greater importance particularly at higher tidal levels. The birds use foot-vibration to increase availability of small Crustacea when this is depressed by adverse weather conditions. Also Dunlin *Calidris alpina* appears to provide the main interference in their use of feeding area at Lindisfarne.

In the following discussion I shall attempt to justify this model by considering the ways in which the birds exploit the behaviour of their prey; the ways in which environmental conditions and other birds may affect prey behaviour, plover feeding rate and plover dispersal; and how the plovers modify their behaviour in relation to these changes. I shall then discuss the apparently visual foraging technique of plovers, first in relation to nocturnal feeding and finally in comparison to the tactile foraging strategy used by many other waders.

Prey behaviour and its exploitation by plovers

It is clear that the depression of the rate of prey capture by plovers at low temperatures is associated with the depression of activity of their prey, *Arenicola*, other worms and small Crustacea, in such conditions. Activity leads prey animals to come within reach of a bird's bill and also, in some cases at least, makes them detectable (cf Davies 1977, for Spotted Flycatchers *Muscicapa striata* which may lose sight of flies when the latter stop moving). Comparable depression of activity with declining temperature has been reported for swimming by *Bathyporeia* (Fincham 1970b, Preece 1971), *Eurydice* (Jones & Naylor 1970) and *Corophium volutator* (Morgan 1975); emergence from the mud by antennae of *Corophium* (Goss-Custard 1969) and from sand by *Talitrus saltator* (Pallaualt 1954); and possibly siphon emergence from the mud by *Macoma balthica* (Goss-Custard *et al.* 1977).

In addition to reducing activity at low temperatures, many animals burrow deeper in the substrate in the winter months (e.g. *Arenicola* - Smith 1975; *Macoma* - Reading & McGrorty 1978; *Nereis diversicolor* - Evans 1979) or move downshore towards the sublittoral zone (e.g. *Arenicola*, *Carcinus maenas*, *Crangon vulgaris*, *Nerine cirratulus* - Brady 1943, Naylor 1962, Swennen 1971, D.M. Brearey in Evans 1979), and

this probably exacerbates the problems for waders in winter. Many invertebrates also move deeper or become less active as the tide falls and the substrate dries (Newell 1962, Vader 1964, Smith 1975, Little & Nix 1976, Evans 1976, 1979, present study) and this probably accounts for the general decline in feeding rates with time after exposure and increasing wind force. For plovers using a space-demanding foraging strategy, there is little scope for avoiding this by moving area in the way that sandpipers do, i.e. following the zone of high availability near the tide edge.

Why should the prey animals make themselves available to birds at any time? Most infauna require access to the surface for food, respiration or other reasons and burrowing is energetically expensive (Trevor 1978), so that it is probably advantageous to remain as close to the surface as temperature or predation considerations allow. Studies of *Arenicola* have shown how the feeding method involving the throughput of large quantities of sand requires that this sand be removed from the burrow and, indeed, the worms appear to be able to achieve this in a short time on each occasion and may have to defaecate on only 2 to 5 occasions during tidal exposure (Smith 1975, Evans 1979).

It is not clear why *Notomastus* makes its migrations to the mud surface as this behaviour does not appear to have been described or investigated previously. A very few occasions of appearance of the head of the worm may have been associated with feeding but whether the outflows result from irrigation for feeding or respiratory purposes is unknown. The mainly nocturnal surface appearances (usually in areas with a thin water covering) of other worms such as *Phyllodoce* and the occasional appearances of syphons of *Macoma* and *Cardium* (also usually in areas with a water covering) appear to be associated with feeding.

It is the brief visits to the surface by polychaetes, such as *Arenicola* and *Notomastus*, that plovers utilize both to bring the worms within their reach and to locate them. By specializing in scanning a large area and being adapted to rapid movement to the site of a cue the plovers are able to utilize a feeding area even if the density of available prey is low. Despite their apparent reliance on visual searching, they appear to be remarkably effective nocturnal hunters and are able

to exploit the nocturnal activity of worms such as *Phyllodoce* and sandhoppers such as *Talitrus* which are presumably night-active to avoid other predators. Presumably the plovers' large eyes are adaptations to this behaviour.

Small amphipods and isopods, notably *Bathyporeia* and *Eurydice*, normally swim mainly when covered by the tide and this activity is generally related to feeding (particularly in *Eurydice*, which preys on *Bathyporeia*) and the achieving of mating contacts (Fincham 1970a, b, Jones & Naylor 1970, Preece 1971). As in the present field study, Preece (1971) found that swimming activity in the laboratory was depressed at low temperatures. Most of these authors found a tidal rhythm which could be modified by environmental conditions. In laboratory studies, Enright (1962, 1965) found that activities of several intertidal amphipods were stimulated by rapid but small changes in hydrostatic pressure and suggested that this was an adaptation to initiate swimming when waves reach the animal as the tide rises or falls. Also in the laboratory, Jones & Naylor (1970) found that only mechanical disturbance of the sand caused the *Eurydice pulchra* to swim and concluded that "it seems likely that in the field wave action must wash them out."

It seems likely that the foot-vibration of Ringed Plovers is exploiting this reaction to vibrations and stirring, as the plovers used this method commonly only in the areas where these small Crustacea were prey and the method was used almost invariably when the birds were feeding on the Sand Rig area where almost all prey were *Eurydice*. There was no difference in feeding rates in a given area between birds foot-shaking and those not but this could be because Ringed Plovers foot-vibrate only when prey are being detected insufficiently quickly without vibration. This is supported by Table 20 which shows that foot-vibration was frequently associated with environmental factors tending to reduce prey activity or feeding rate. Like other aspects of plovers' behaviour, foot-vibration is clearly not adapted solely to particular prey types (see also Paper 1). Simmons (1961), Sparks (1961) and Swennen & van der Baan (1959) have described and reviewed some of the occurrences of the various types of foot-movement in plovers and other birds. Some plovers use a similar technique in the very different

terrestrial situation of feeding on earthworms *Lumbricus* and *Allolobophora*. It has been suggested (without strong evidence) that the earthworms react to the vibrations as if they were caused by rain and emerge from their burrows; also that similar vibrations are caused by moles and the worms ascend to avoid falling into mole tunnels (see Simmons 1961). It seems likely that the technique may be applied in any situation, its use being continued if profitable. The occasional - and unmaintained - occurrence of foot-shaking on the Low Flats of HIS would be compatible with this interpretation. Contrary to Simmons (1961) and in agreement with Swennen & van der Baan (1959) and Sparks (1961), in the present study worms were not taken when foot-vibration was used intertidally. As suggested by Sparks, it is used when small Crustacea are the main prey, although the way in which it makes them more available appears to depend at least partly on the animals' normal reaction to waves and tide, rather than only by producing a semi-fluid water/sand mixture by thixotropy, thus causing the animal to swim.

Environmental effects on feeding rate

If prey availability is limiting capture rate, an increase in the latter should be expected as the former increases. Any such relationship may, however, be complicated if the degree of prey selection varies with prey availability. Various theories of optimal foraging strategies predict that selectivity in choice of prey should increase when density of available prey increases (e.g. Emlen 1966, MacArthur & Pianka 1966, Schoener 1971, Pulliam 1974). On this basis, and if one assumes that energy intake per unit time is to be maximized, then large prey should become increasingly large components of the diet as they become more available. Therefore, one would expect the rates of capture of the largest prey (*Arenicola* for Grey Plovers and large *Notomastus* for Ringed Plovers) to increase with increased availability of these prey but the rates of capture of alternative prey to depend both on their own availability and that of preferred prey. Goss-Custard (1977c) described a comparable situation in which the feeding rate of Redshanks on small worms was more influenced by the density of large worms (and biomass of these ingested) than by the density of small worms. The feeding rates of plovers on various types of prey in relation to environmental conditions at Lindisfarne are summarized in

Figure 20 and discussed below.

Feeding on *Arenicola*

Generally the feeding rate of Grey Plovers on *Arenicola* increased with increasing temperature and decreased with increasing wind force and time after high water. These relationships are all compatible with the observations of *Arenicola* behaviour described by Smith (1975) and summarised above. In some situations, the rate of capture of *Arenicola* increased with increasing cloud cover. The reason for this is less apparent but could be related to slower drying of the sand surface when out of direct sunlight, as *Arenicola* activity is reduced as the surface dries. Alternatively, increasing cloud cover may reduce glare off the wet sand surface as suggested in relation to foraging by herons (Krebs & Partridge 1973, Krebs 1974).

The higher feeding rate of Grey Plovers on *Arenicola* in spring than in autumn and winter on the Low Flats may be related to the early departure of Bar-tailed Godwits *Limosa lapponica* from Lindisfarne in spring. After numbers of Godwits dropped the Grey Plovers spread nearer the tide edge and at times fed in water. At Teesmouth also, Grey Plovers left areas as Godwits and Curlew *Numenius arquata* moved in (Pienkowski 1973, 1980).

Feeding on *Notomastus* and other thin worms

In Ringed Plovers at low temperatures, the increase in rate of capture of thin worms with mud temperature (Figs. 6, 7, 20; Table 4) probably reflects the increasing activity of the worms as temperatures rise (Fig. 3) and the depressing effect of increased wind may reflect depression of worm activity by increased drying, reduction of visibility of cues due to increased movements of water in the surface film, or increased difficulty experienced by the plovers in making rapid directed movement in such conditions. At higher temperatures feeding rate declined again in spite of continuing increase in prey activity but the mean size of worm taken continued to increase and it is likely that the plovers became more selective of larger worms. Curves of comparable shape were obtained by Hulscher (1976) relating the rate of taking of cockles *Cerastoderma edule* by Oystercatchers *Haematopus ostralegus* to the density of cockles, and by Goss-Custard (1977d) /~~for~~/

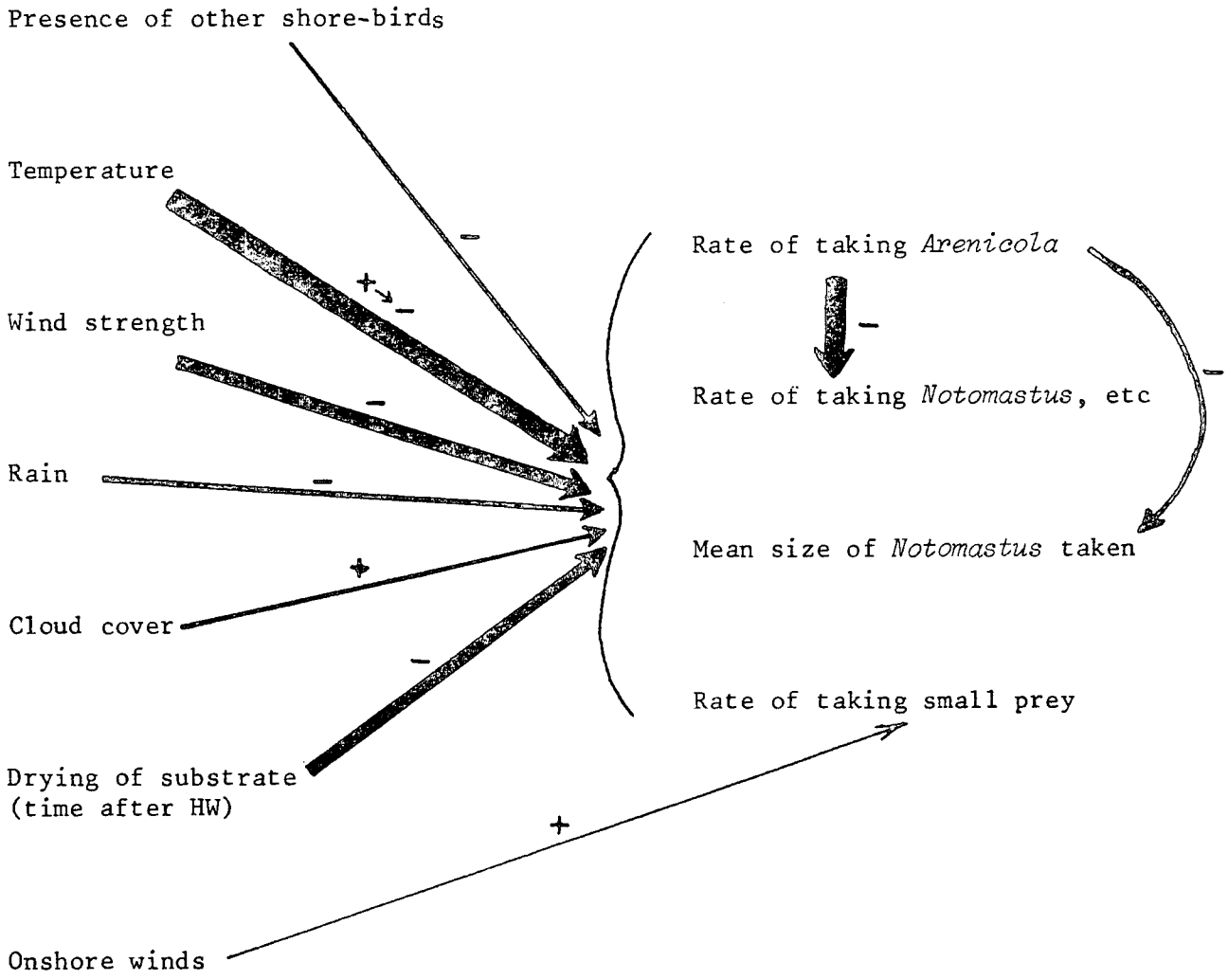


Figure 20. Summary of correlations between feeding conditions and feeding rates. Approximate strength of correlations indicated by thickness of lines

for the rate of capture of *Corophium* by Redshanks *Tringa totanus* to the density of *Corophium*.

The estimated rate of occurrence of outflows in the search area of Ringed and Grey Plovers are compared with rates of taking thin worms in Figure 21. As well as showing the rates from sites A/B and C/D, Figure 21 includes an estimate of the presumed rate at a density of half that of sites C & D. This estimate should be more typical of the whole of the feeding area on Low Flats as the activity observations were concentrated at the areas of highest density. The suggested transition to selection of increased size of worms by Ringed Plovers at about 6°C coincides with the divergence of feeding rates and outflow rates, suggesting that below this temperature, the plovers were indeed pecking at almost all outflows. (Note that few outflow observations are available below 4°C so that the regression may be less applicable there.) In Grey Plovers, the estimates coincide at about 4°C. The difference between the numbers of outflows per minute and rate of capture of worms suggest that the Grey Plovers are generally more selective than Ringed Plovers in pecking at outflows.

Although estimations of total calorific intake are not accurate enough for very precise analysis, the increase in worm size appears to compensate for the reduction in their rate of capture (Fig. 22). (Because the calorific value of largest thin worms is probably underestimated (see Paper 1) the rate of calorific intake at high temperatures is probably also underestimated slightly.)

At higher temperatures on the Low Flats the rate of taking thin worms declined with time after high water but mean worm size increased (Table 4). Possibly some degree of drying of the substrate aids estimations of the size of worms from the diameter of the holes or of the outflows of water, if these are the cues used. On the High Flats both rate of capture of thin worms and mean worm size declined with time after high water, presumably due to drying of the substrate (cf Fig. 4). This is supported in that onshore winds (which tend to keep a film of water on the upper flats of HIS) were associated with increased rate of taking worms. (Note, however, that because of the method of estimation of rate of capture of thin worms it is possible

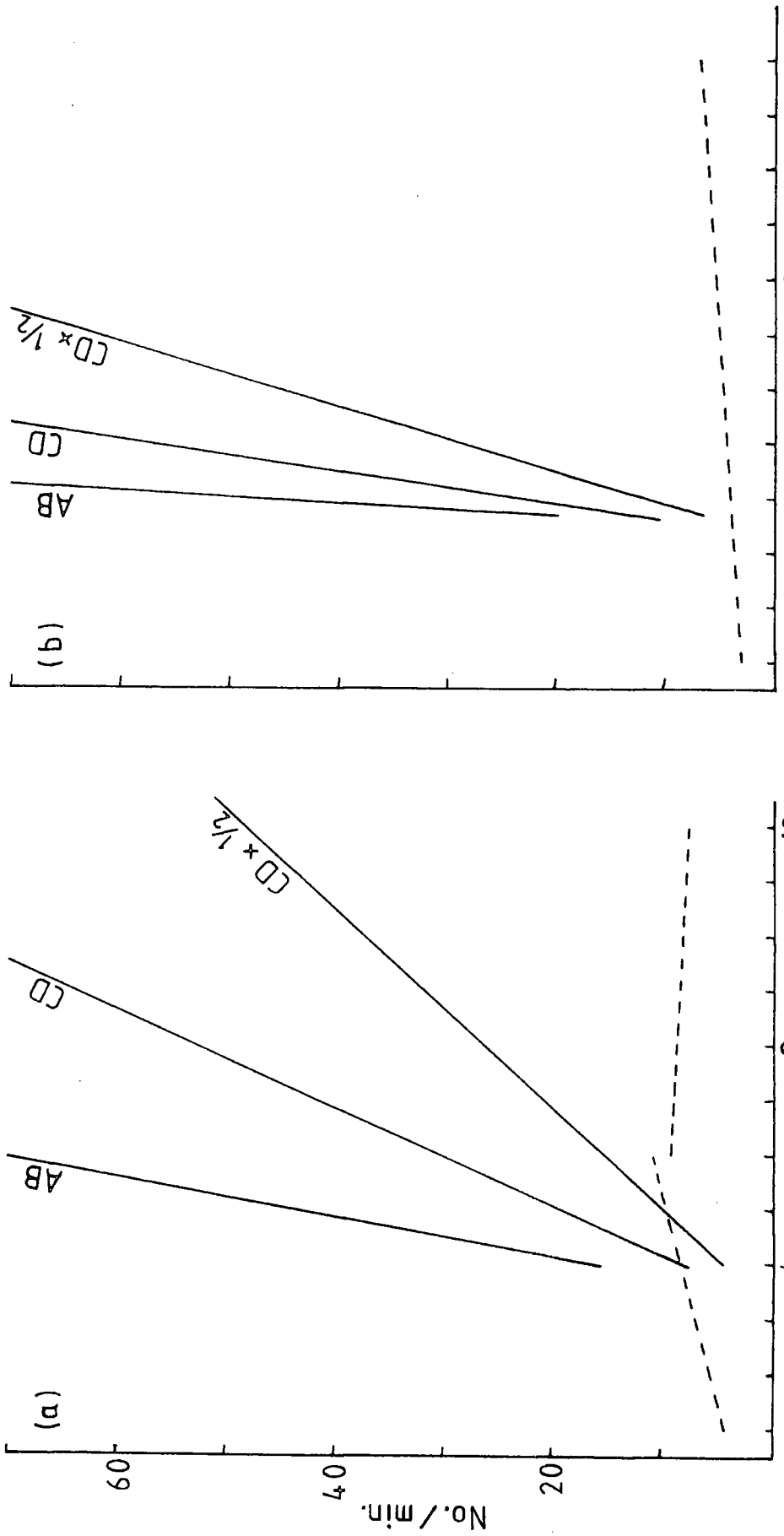


Figure 21. Estimated numbers of outflows (solid lines) in search areas of (a) Ringed Plover and (b) Grey Plover on the Low Flats in relation to temperature, and estimated rates of taking thin worms (dashed lines). Solid lines are based on Figure 3.

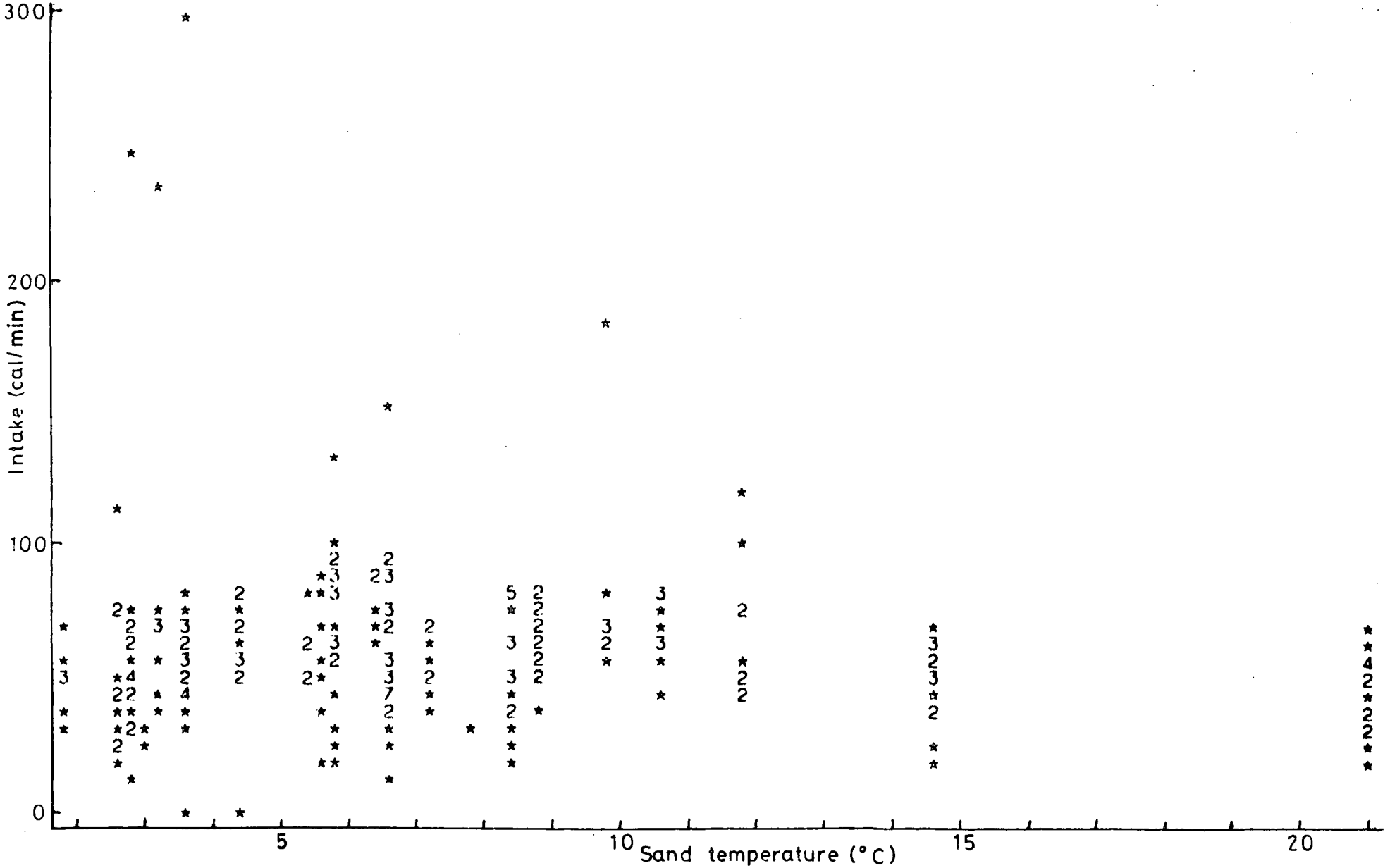


Figure 22. Estimated rate of calorific intake of Ringed Plovers on the Low Flats in relation to sand temperature. The few points of high intake are due to the occasional taking of *Arenicola*.

that inclusion of some small prey in this estimate may influence the relationships; onshore winds also increase the rate of capture of small prey, possibly by concentrating small Crustacea into this area.) The rapid movement of Ringed Plovers from the High Flats as tide falls is probably associated with the depression of intake rate there as well as the exposure of the Low Flats with higher worm densities.

For Grey Plovers the rate of capture of thin worms appeared to be depressed as the rate of taking *Arenicola* increased. Such a decrease might be expected simply because the long handling times for *Arenicola* would reduce the effective foraging time for other prey. However, the reduction in thin worms taken was greater than expected from this (Fig. 14, $P < 0.001$ for Low Flats in spring; $P < 0.05$ for Low Flats in autumn and winter; not significant in High Flats due to low frequency of *Arenicola* taken) and this suggests that in such situations the plovers were modifying their behaviour to take *Arenicola* so that thin worm cues were either not seen or largely ignored.

In such situations, the rate of capture of thin worms would be expected to decrease even more than indicated by the rate of capture of *Arenicola*. This is because, due to the low rate of taking *Arenicola*, this prey may not be recorded during many observation cases when it is the main object of foraging. This would account for the increase of rate of capture of thin worms in spring on the Low Flats with falling temperature, rising wind strength and increasing time after high water as all these lead to decrease of *Arenicola* activity and presumably increased attention to thin worms.

In autumn and winter, fewer *Arenicola* were taken and while the capture of *Arenicola* is still inversely associated with the rate of capture of thin worms, the relationships between rate of capture of thin worms and environmental factors correspond more closely with those expected from direct considerations of thin worm behaviour.

Similarly throughout the season on the High Flats, where fewer *Arenicola* were taken than in spring on the Low Flats, the rate of taking thin worms and the mean worm size generally showed similar relationships with environmental conditions as for Grey Plovers in

autumn and winter on the Low Flats and Ringed Plovers in all situations, but increased rates of taking *Arenicola* still appeared to depress rate of taking thin worms.

A comparable situation in which the number of small prey items taken by Redshanks was influenced by the density of large worms as well as of the small prey has been described for Redshank by Goss-Custard (1970c, 1977c, 1978). This comparison was based on observations in different sites or experimental situations, rather than in relation to variations in temperature-dependent availability as in the present case. Smith (1975) working on Bar-tailed Godwits at Lindisfarne and Goss-Custard (1969) studying Redshanks at the Ythan estuary, NE Scotland, also detected changes in diet corresponding to temperature effects on the availability of their prey. Selection for particular prey species has been suggested for Redshank by Goss-Custard (1977a) but this selection resulted in maximum biomass or calorific intake per unit time only when *Corophium*, the preferred prey, was considered. *Corophium* was preferred to the much larger *Nereis*, and Goss-Custard suggested that, in detecting inconspicuous cues by visual means, Redshanks might form search images limiting the range of cues that were noticed. The apparent selection by Grey Plovers of *Arenicola*, when these were available, over small worms fits better expectations based on biomass intake and this may be a reflection of the ability of a specialised visual forager (Grey Plover) to respond to visual cues, in comparison with the ability of a more generalised shorebird (Redshank). Indeed, there is no reason to suppose that specialization on a particular foraging method necessarily implies specialization on particular types of prey (*contra* Baker 1974).

Feeding on small prey

As might be expected from a consideration of prey behaviour (Fig. 5), the rate of taking small prey by Ringed Plovers on the High Flats near the small salt marsh increased with increasing temperature and with decreasing wind force at low temperatures. As for the rate of capture of thin worms, there was a decline in rate of capture of small prey at higher temperatures. The conditions during observations did not allow investigation of prey size for small prey, so any effects of size selection within this prey category could not be detected. However,

selection for large thin worms was probably taking place in this feeding situation (see above). At low temperatures, but not at high, the rate of capture of small prey was lower on the rising than on the falling tide, presumably because of drying of substrate. Inspection of Figure 9 suggests a rising rate just before HW as the tide wetted the area. At high temperatures, no tidal pattern in rate of prey capture was found, perhaps because at these temperatures prey activity is above a 'plateau' level for maximum rate of taking prey by the plovers.

Most of the amphipods drift to some extent in the water when the tide is high. Presumably the extent to which they are concentrated up and/or along the shore depends on the wind direction. One might expect higher densities to be left after onshore winds and this may be the explanation of the higher feeding rates near the small salt marsh during winds between SE and W. On the North Shore, a narrow channel separates a N facing shore on the Snook and a S facing shore on the Rig so that one would not expect a great difference in feeding rate according to wind direction and, indeed, none was found (Table 6). However, the mean rate here was somewhat lower than on the flats during onshore winds, possibly because, on the latter area, winds concentrate prey from a wider area at the top of the shore.

The present results contrast with those of Baker & Baker (1973) who found for several species of waders very few relationships between pecking rate and air temperature, number of conspecifics and number of other shorebirds near. The waders they studied included Semipalmated Plover *Charadrius semipalmatus* which is closely related to Ringed Plover. However, the temperatures during their study were much warmer than in my study. Baker (1974), working on Black-bellied Plover (i.e. Grey Plover) on autumn and spring migration in Connecticut, found a weak positive correlation between the proportion of capture attempts that were successful and temperature, although the temperatures were again somewhat higher than in the present study.

As in the present study, Townshend (in Evans 1976) also found a decrease in feeding rate of Grey Plover on *Nereis diversicolor* at Teesmouth as wind strength increased, In other studies, strong winds have been found to cause birds to congregate in sheltered feeding

sites or stop feeding altogether (Evans 1976, Goss-Custard 1976, Dugan *et al.* in press).

In some situations in the present study, the rate of prey capture, particularly of thin worms, decreased with increasing rainfall. This may have been due to difficulties experienced by birds in distinguishing the impacts of rain drops from prey outflows, difficulties also experienced by human observers. Goss-Custard (1970a) noted a similar depression in feeding rate of Redshanks *Tringa totanus* on *Corophium* in rain. He also found that simulated rainfall depressed the number of *Corophium* appearing at the surface.

Proximity of other birds

Feeding plovers of both species appeared to avoid concentrations of other shorebirds and after most Bar-tailed Godwits had left in spring the prey intake rate of Grey Plovers, at least, increased. A comparable situation occurs for Grey Plovers at Teesmouth (Pienkowski 1973, 1980, Goss-Custard *et al.* in prep.). At Ventjager, the Netherlands, Avocets *Recurvirostra avocetta* and Black-headed Gulls *Larus ridibundus* avoid each other while feeding, and for several species of shorebird there was evidence that birds avoided high densities of conspecifics by moving to less preferred areas when numbers were high (Zwarts 1974). The latter conclusion was supported by more detailed evidence for Redshank in the Ythan estuary, Scotland, by Goss-Custard (1977d). However, other shorebirds are generally more tolerant than plovers to high bird densities.

Smith (1975) found that, in the infrequent antagonistic interactions between species during feeding, Grey Plovers were displaced by Bar-tailed Godwits. It seems likely that high bird densities, by restricting the area of view, could cause difficulties in the plovers' normal foraging method, which depends on having a large enough area available per bird to give a reasonably high frequency of surface activity within that area, whereas long-billed, tactile foragers can search a small area profitably by taking prey not only at the surface (cf Goss-Custard 1976). It is also possible that a high density of birds impedes the rapid runs normally made by plovers to prey (cf the suggested mutual interference of movement in feeding Teal *Anas crecca*

- Zwarts 1976). High numbers of birds may also depress surface activity of invertebrates as found for *Corophium* by Goss-Custard (1970a). Mechanical disturbance or pressure on the substrate surface also appear to reduce surface activity of *Nereis* and siphons of *Macoma* (Goss-Custard 1970a; pers. obs.). Visual searchers would probably be affected more by such a reaction of the prey than tactile searchers (cf Goss-Custard 1970a, Zwarts 1974, Pienkowski 1980). Comparable inter- and intra-specific avoidance has been described and discussed by Zwarts (1974).

Decreased feeding rate of both species of plovers in all conditions tended to be associated with increasing flock-size and increasing distance to nearest neighbour. While it is possible that increasing flock size impedes plover feeding in the same way as the presence of large numbers of other birds may do, this seems unlikely for two reasons. First, the flocks are well spaced, and second, the relationship of feeding rate to nearest-neighbour distance is the opposite of that which an interference hypothesis would suggest. An inverse relationship between nearest-neighbour distance and feeding rate has been found for Redshank but only at unusually high densities (Goss-Custard 1976, 1977d). Also, the closer crowding of plovers would of course affect all the birds concerned, which is not the case when sandpipers crowd plovers. Possibly increased flock-size allows greater protection against birds of prey which are important predators in at least some situations and which appear to be more successful against solitary shore-birds than against flocks (Page & Whittaker 1975, Smith 1975, see also e.g., Davis 1975, Lazarus 1979 and other workers cited there). Flocking may aid defence after detection of predators by confusion of predator or by the reduction in the probability that any one individual bird will be caught (e.g. Hamilton 1971, Vine 1971, Pulliam 1973, Owens & Goss-Custard 1976).

An alternative explanation for the inverse correlations between feeding rate and flock-size is that, when feeding rate is low, plovers concentrate in the best feeding areas. This would be compatible with theories of social facilitation, local enhancements and flocks acting as information centres (e.g. Murton 1971a,b, Krebs *et al.* 1972, Ward & Zahavi 1973). A comparable aggregation on the richest feeding areas by

Oystercatchers at Strangford Lough, N. Ireland, during the winter as densities of available cockles *Cerastoderma edule* were reduced (in this case by predation) has been described by O'Connor & Brown (1977). At Lindisfarne in very cold weather Smith (1975) found a concentration of Godwits at the best feeding areas (i.e. at the tide edge), leading to an increase in agonistic interactions. Possibly the correlation between decrease in feeding rate and increase in nearest neighbour distance in plovers is the result of the concentration of birds in the sites of highest density of available prey, while concurrently leaving sufficient space for efficient foraging. This could parallel the study of foraging of Great Blue Herons by Krebs (1974) who also demonstrated how birds would tend to concentrate in the best feeding areas as the result of a balance between steady arrival rates and varying departure rates, the latter influenced by giving-up times (i.e. the time duration which a bird would wait before moving to a new site).

The plovers seem to pack more closely as the distances moved while foraging decrease (Table 14 and night observations). Such a compromise between the requirements of anti-predator defence and feeding efficiency has been discussed by Goss-Custard (1970a) and Lazarus (1972). In the case of the wide search areas of plovers, looser flocks are required for efficient feeding but these become tighter as feeding rates increase and food is obtained closer to the birds, or at night when effective foraging range appears to be reduced.

Changes in foraging pattern with environmental and flock conditions

The relationships of diet and feeding rates with environmental and flock conditions suggest that in cold and other adverse conditions the feeding rate of plovers is governed by the activity of the prey but as conditions become more favourable the birds become more selective for larger items and prey types. Plovers may feed more closely together in areas of high density of available prey. The feeding areas exploited and thus the prey types taken may be influenced by the presence of competing predators which can forage at higher densities. This general model (summarized in Figure 23) receives some support from a consideration of how the birds modify their foraging behaviour according to the feeding situation.

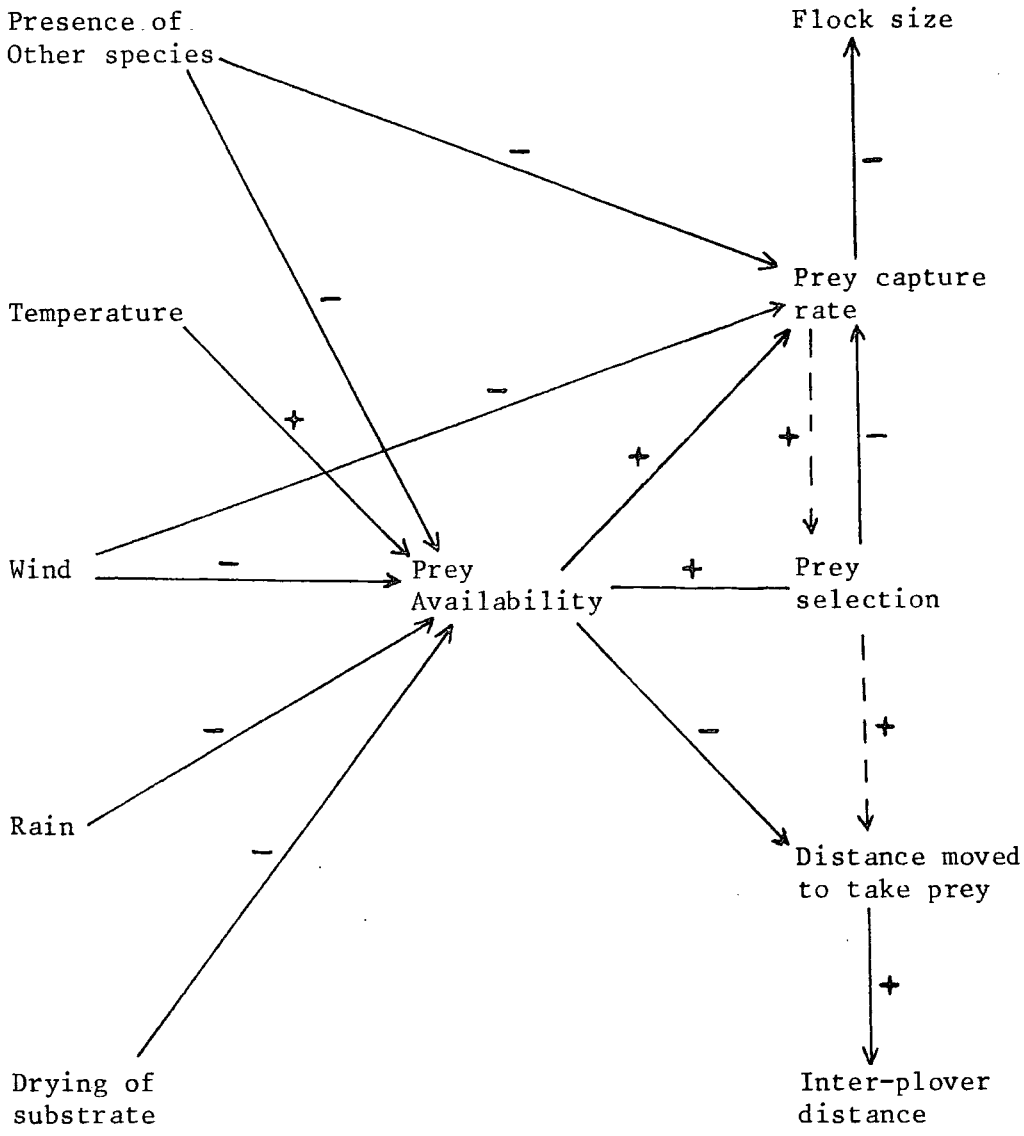


Figure 23. Schematic model of the effects of environmental conditions and the presence of competing species on plover feeding rates, prey selection and bird distributions.

On the Low Flats the mean distance moved between 'up' positions by Ringed Plovers did not change with environmental conditions whereas at high tidal levels the distance moved increased with changes in factors associated with reduction in prey activity and feeding rate. Possibly in such adverse conditions on the High Flats, the birds' movements enabled the sampling of a wide area to detect concentrations of mobile prey where prey distribution varies in a fairly unpredictable manner from tide to tide.

For Grey Plovers on the Low Flats the mean distance moved between 'ups' increased with those factors which led to increased feeding on *Arenicola* (as opposed to other prey) and, indeed, with the rate of taking *Arenicola*. This probably results from the greater range from which the birds may move to take *Arenicola*: consequently a larger area will be scanned from one waiting position, leading to a greater distance to the next vantage point. On the High Flats where fewer *Arenicola* were taken, the distance moved increased with decreasing temperature, possibly for analogous reasons to those suggested for Ringed Plover, i.e. sampling a wider area. A comparable increase in distances run between pauses when prey were presumed to be less available was recorded at Teesmouth by D.J. Townshend (in Evans 1979).

For Ringed Plovers on the Low Flats the mean number of paces moved to peck at prey generally decreased with those factors leading to increased pecking rate and prey availability as might be expected if the birds tend to take suitable prey nearest them. On the High Flats, no trend with physical conditions was apparent. If there really is no trend, this could be due to the short range at which the small prey in this area could be detected or because, in the clumped areas in which prey do occur, they do so in fairly high numbers.

For Grey Plovers on the Low Flats the distance moved to take prey increased with rate of taking *Arenicola* and from winter to spring, both relationships probably being due to increased foraging on *Arenicola* to which the birds may move greater distances than to other prey. J.N.M. Smith (1975) noticed an increase in movement to take prey when more conspicuous artificial prey was provided experimentally for Blackbirds *Turdus merula* and when grass was cut short, this also increasing

conspicuousness of prey. Distances moved by Grey Plovers to take thin worms increased with environmental factors associated with increased foraging on *Arenicola* and distances moved to take small prey increased with rate of taking *Arenicola*. This could suggest that such prey are taken incidentally during foraging primarily for *Arenicola*.

In several situations for both species, the distances moved to a new position or the distance moved to take prey increased significantly with increasing distance to the nearest other bird of the same or other species or decreasing flock-size. If, as suggested above, increased movement is associated with reduced prey availability, and increased flock-size and nearest neighbour distances with reduced feeding rates, these sorts of relationships would be expected.

The maximum numbers of paces normally moved to take most prey appear to remain fairly constant in different conditions (Table 16); about 3 for Ringed Plovers and about 4 for Grey Plovers (although more when taking *Arenicola*). This may correspond to the maximum range of detection or the maximum distance to which the bird can move and catch the prey while it is still available. These distances also appear to correspond fairly well (particularly after adding the 1 pace corresponding to the distance reachable without moving farther) to the mean distances moved to a new waiting position: 4.0 and 5.3 paces for Ringed Plovers on Low and High Flats respectively, and 5.4 and 7.8 for Grey Plovers. This suggests that the plovers move on just far enough to scan a totally new catching area when the viewing position is changed (see Fig. 19). But in some situations possibly of lower prey density or availability and lower feeding rates, such as parts of the High Flats, the birds may move further in their search for prey concentrations.

Table 15 demonstrates that when prey are taken the bird moves less far to the next waiting position and that the distance moved decreases with increasing size of prey. This behaviour would be adaptive if prey distributions were clumped, as indeed they tend to be. Such a reaction to a high rate of food intake leading to a concentration of feeding waders on areas of highest food availability was suggested for Redshanks by Goss-Custard (1970b) but he had no data then to test this. Baker

(1974) found that success of a given predation attempt by Black-bellied Plovers shortened the subsequent distance travelled compared to that after unsuccessful attempts. J.N.M. Smith (1975) found that Blackbirds *Turdus merula* and Song Thrushes *T. philomelos* altered their foraging path after capturing an earthworm or artificial prey (each of whose dispersions were aggregated) to concentrate their activity in the vicinity. This also applied to randomly but not regularly spaced artificial prey. Krebs (1973) gives further examples of "area-restricted" searching.

Generally the waiting time before taking prey increased with decreasing size of prey. This is at first sight surprising in that, for example, in both Grey Plover feeding areas, cues for *Arenicola* tended to be less frequent than those for thin worms, and the feeding rate on *Arenicola* was less than for thin worms. Similarly, for Ringed Plovers on the High Flats, cues for small prey were more frequent than those for worms and, on the Low Flats, cues for small thin worms (which are included in small prey in this comparison) were more frequent than those for larger thin worms. In both areas the feeding rate on visible thin worms (those for which waiting time is allocated to worms) was less than the feeding rate on small prey. This apparently anomalous result could be accounted for if, in a given waiting period, the plover initially tends to ignore cues of small prey but becomes progressively more ready to react to them. For example, a Grey Plover is initially responsive mainly to *Arenicola* cues but becomes progressively more responsive to thin worms (probably first large ones and later increasingly smaller ones) and later increasingly to small prey. Finally the bird becomes increasingly liable to give-up, the giving-up time being slightly longer than the waiting time for small prey.

An alternative strategy of responding to the first cue seen would result in small common prey forming the diet and larger prey rarely contributing. By allowing time for large prey to appear but being progressively more ready to take smaller prey, some intake is likely, larger intake if available is allowed for and the sampling of as many areas as possible results. Because the small handling time of small prey involves very little extra time over that simply to move site (Table 8) taking a small prey does not involve much 'cost' in foraging time.

The tendency for waiting and giving-up times to be correlated (Table 10) suggests a strategy rapidly flexible in relation to local conditions, possibly analogous to the rapid appearance of selection of preferred prey size by Redshanks in an experimental situation (Goss-Custard 1970c).

In Ringed Plovers, both giving-up and waiting times tended to decrease with increasing temperatures to about 4 - 6°C and then increase again. This probably corresponded to the increased availability of prey and the suggested increased selection of larger worms discussed above. On the High Flats 'up' times of Grey Plovers also increase with increasing temperature and increased rate of taking *Arenicola*, probably the result of increased foraging on *Arenicola*. In some situations for both species of predators, the waiting times increased with wind-force, presumably the result of increased difficulty in foraging. Little consistent pattern was apparent in the relationships with rainfall or cloud cover.

In Ringed Plovers, waiting times tended to increase later after high water, presumably as areas dried out and prey became less available. In Grey Plovers on the Low Flats the reverse tendency showed, possibly as the birds transferred their attention from *Arenicola* to thin worms as the former became less available.

Little consistent variation was indicated in relation to flock-size or nearest-neighbour distance.

The rate of occurrence of 'downs' appeared to be associated with conditions leading to the increased selection of large thin worms: increased temperature, decreased wind force, increased flock size, decreased nearest-neighbour distance and, in Grey Plover, later in the tide and decreased rate of taking *Arenicola*. The capture of an *Arenicola* was less likely to be preceded by a 'down' than was the taking of a thin worm.

The present results have some similarities to those discussed by Krebs & Cowie (1976) in relation to the model of Charnov (1976) except that, in the present case, rather than monitoring depletion the bird

should be assessing the probability of activity in non-randomly dispersed prey in the search area. The earlier experiments by Krebs *et al.* (1974) in which prey depletion was not incorporated are therefore more similar to the present field situation. Like the Black-capped Chickadees *Parus atricapillus* in that study where the reciprocal of giving-up times were closely related to the capture rate, the giving-up times and waiting times of the plovers at Lindisfarne were correlated.

The situation where there is negligible depreciation during a particular feeding period and where changes in prey availability are largely independent of the predator's activity, as usually applies in the present study, has also been studied in the field by Davies (1977) working on Spotted Flycatchers, another predator foraging in a basically sit-and-wait manner. Davies showed that the probability that a bird will return to the same perch is negatively related to the waiting time before the last capture. This has parallels with the patterns of giving-up time and distance moved in relation to prey taken in the present study in that plovers move farther after taking no prey or small items than after capturing larger ones, and waiting time is inversely related to the size of prey taken.

Nocturnal foraging and senses used

It has frequently been supposed that, when feeding at night, plovers are at a considerable disadvantage when compared to other waders which appear to rely mainly on tactile location of prey in darkness (e.g. Goss-Custard 1970a, Hulscher 1976). Hulscher found that, although foraging methods of Oystercatchers changed from daylight to darkness, the rate of biomass intake did not - but the average energy costs of each foraging method are unknown, hence the relative rates of net intake in the two situations are unknown. Plovers have commonly been noted in the feeding areas during darkness and observations at Lindisfarne using night-viewing apparatus showed that they were able to feed even on overcast and moonless nights, either by utilising the very low light intensities available or by detecting their prey by sound. It is also possible that plovers detect prey tactilely using their feet but this is unlikely as prey were rarely taken from the immediate vicinity of the feet, where they were presumably hidden to the birds' sight by their bodies.

Perry (1945) considered that plovers at Lindisfarne foraged by hearing but his opinion was based only on the birds' stances. Several authors have assumed acoustic abilities by foraging plovers (see review by Lange 1968) and Fallet (1962) presented some evidence that Golden Plovers in captivity could locate prey by hearing. She suggested that the two pauses (= up, (run), down, (run), before peck) enable this to be done. However, in many situations, as in the present study, 'downs' were infrequent. The fact that they were particularly so at night (Tables 21, 22) when one would expect maximum use of acoustic prey location suggests that these are not auditory aids. The latter view is supported by Burton (1974) who saw 'down' positioning used by the White-tailed Lapwing or Plover *Vanellus leucurus* in Iran. As the bird was hunting prey submerged under water, it would hardly have used auditory cues.

Lange (1968) and earlier authors suggest that because plovers sometimes turn to take prey from behind them, this is evidence of acoustic detection, as such prey positions are outside the range of vision of plovers. However, the present study demonstrates that pecks behind are rare (Fig. 18). In any case, the large eyes of plovers placed at about the widest part of the head give almost all-round vision, and the tapering of the front of the head towards the bill allows additionally good binocular vision forwards.

However, Lange (1968), although conceding the importance of visual foraging, presented experimental evidence of acoustic detection of prey by a wide range of captive waders including several species of plovers. The evidence that plovers in cages could detect large, noisy prey, earthworms Lumbricidae and mealworm *Tenebrio* larvae, by auditory means does not show that in field situations they normally use or are able to use such a technique on the smaller prey being taken there. Heppner (1965), working on the American Robin *Turdus migratorius*, which forages in a manner similar to plovers, concluded that earthworms were located only by visual means. In various experiments he found evidence for visual searching, but none supporting auditory or olfactory detection. In particular the rate of capture of earthworms was not affected by the presence of high-intensity white noise and the background noise in the normal situation masked the low intensity of sounds

made by burrowing earthworms. Prospects for audible detection of the smaller worms and other prey on open shores with a background of wind and wave noise thus appear unpromising, possibly except for very noisy prey, such as *Talitrus*, on calm nights away from the tide edge (see also Evans 1976).

Whether or not audible cues are used, it appeared that pecking rate was depressed on dark nights but perhaps not on light ones, so that nocturnal feeding appears less rewarding. When feeding at night, the distance moved to take prey tended to be shorter and the percentage of prey items taken without taking paces increased. This was so even when overall pecking rate was not depressed, and it suggests that the range of prey detection was depressed and possibly that the birds were less selective as to the types of prey taken. The rate of occurrence of 'downs' was also depressed at night suggesting fewer long-distance detections of suitable prey. Waiting time tended to increase, possibly because fewer prey were detected per unit time, but in Grey Plover giving-up time did not. Possibly this was related to the tighter flock structure observed at night, the birds surveying the area as a flock rather than as individuals. Presumably the shorter potential range of prey detection in darkness allowed the closer flock formation, since in daylight also shorter distances moved to prey were associated with closer proximity of other birds.

Although nocturnal foraging appears to present more difficulties than daylight feeding, and plovers and other birds appear to avoid it when it is possible to obtain their requirements by day, energetic considerations (Paper 1) clearly indicate that a great deal of feeding by night must occur in winter. Possibly, other factors may compensate for limitations in the range of prey detection. Among these may be increased prey activity.

In terrestrial situations, earthworms tend to be more active on the surface at night than by day (e.g. Buchsbaum 1951), and this may be the reason for the high degree of nocturnal foraging noted in Lapwings *Vanellus vanellus*, Golden Plovers *Pluvialis apricaria*, and Snipe *Gallinago gallinago* (e.g. Burton 1974). The defaecation rate of *Arenicola* at night has not been investigated. Grey Plovers were not

seen to take *Arenicola* during night observations although any taken would probably have been visible; probably reasonably large detection ranges are needed for effective feeding on *Arenicola* above the tide edge because of the low density of available prey. (Indeed Smith (1975) did not see Godwits taking *Arenicola* at night, although the taking of a *Nereis* was seen.) The activity of *Notomastus* as indicated by outflows from holes appeared to be similar by day and night but the emergence of *Phyllodoce*, a worm of approximately similar size, apparently to feed for extended periods on surface organisms was far more common at night and in some instances the prey taken apparently caused sections of these worms to become luminous. It seems likely that the plovers may have added these worms to their diet at night. Vader (1964) also found that *Phyllodoce* and some other intertidal errant polychaetes appeared on the surface more at night than by day. Finally, it is well established that many Crustacea of intertidal flats, e.g. *Eurydice* (Jones & Naylor 1970), *Bathyporeia* (e.g. Fincham 1970a,b, Preece 1971), *Talitrus* (e.g. Geppetti & Tongiorgi 1967, present study) are more active by night than by day.

Presumably concentration of activity into the hours of darkness by such shore invertebrates is an anti-predator adaptation (although Eltringham (1971) considered avoidance of harmful ultra-violet and infra-red radiation as the main cause). Although the tendency to nocturnal activity of invertebrates is usually attributed to an adaptation against fish or marine invertebrate predators, behavioural studies have shown that many intertidal invertebrates are able to distinguish between when the tide is in and when it is out, so that some other adaptation is likely in the latter situation. It is, therefore, likely that the avoidance of emergence and activity in daylight around low water is an adaptation to the 'terrestrial' element among the predators, and birds are the main component of this (see also Naylor (1958) and Kitching & Ebling (1967) for activity rhythms of and gull predation on *Carcinus*, other crabs and starfish).

It is possible that plovers, rather than being at a particular disadvantage at night as compared with sandpipers, are in some ways pre-adapted to nocturnal feeding. The Charadriidae are mainly a low latitude family, many of which forage in semi-desert conditions. In

such habitats most potential prey are active only at night, because of the heating and dessicating effect in daylight as well as predation, and many plovers feed by night as well as by day (e.g. Thomson 1964). The large eyes of plovers are probably an adaptation to visual foraging, and possibly nocturnal foraging in particular.

Plover and sandpiper strategies

In the non-breeding season, the behaviour of a bird should be adapted to survival when times are hard. For intertidal waders their behaviours should ensure that they can obtain adequate food supplies when prey are hard to come by: at low activities, deep in the substrate or at low densities. In 1977, I put forward a simple model contrasting the way in which visual sit-and-wait predators, 'plovers', and tactile searchers, 'sandpipers', tackle these problems (Pienkowski 1980). With the further information now available in this and Paper 1, it is possible to develop this model, although, because of the large number of estimations and assumptions required, it remains highly speculative.

The estimated daily energy requirements for Dunlin, Ringed and Grey Plovers and Bar-tailed Godwits are given in Table 23. The factor x BMR for each species is the best currently available. All fall between 3.5 and 5. Changing the value for any species within this range would affect the absolute values of requirements estimated below but would not alter the general pattern. Ratios of night feeding rate to daylight feeding rate are also given, based on the following information. The ratio for plovers is based on Tables 21 & 22 and may be 'pessimistic' from a plover's point of view. It is assumed that tactile foraging of sandpipers is unaffected by light levels, so that feeding rates are similar by day and by night. This received some support from Hulscher (1976) but is probably slightly optimistic. Because of this difference in ratio of night : day feeding rate between plovers and sandpipers, in mid-winter (when hours of darkness are longest and conditions therefore most difficult for feeding), in a situation where feeding for all the time when flats are uncovered is required, plovers should seek to obtain half of their daily food requirement in daylight and half in darkness, whereas sandpipers feeding only by touch (a condition never fully realized) could spread their daily intake uniformly throughout the hours of daylight and darkness, thereby

TABLE 23. ESTIMATION OF REQUIRED FEEDING RATES AT LINDISFARNE (see text)

	DUNLIN	RINGED PLOVER	GREY PLOVER	BAR-TAILED GODWIT
Approximate Lean weight (g)[1]	50	62	212	295
Basal metabolic rate (kcal/day)[2]	9.0	10.5	25.5	34
Daily requirement (x BMR)[3]	4	3.5	3.5	5
Daily requirement (kcal)	36.0	36.8	89.3	170
Assumed mean night feeding rate/ mean daylight feeding rate	1	0.5	0.5	1
Midwinter daylight period as % of 24 h	33%	33%	33%	33%
Minimum proportion of food requirement in daylight if feeding all available day & night	33%	50%	50%	33%
Minimum daylight requirement (kcal)	12.0	18.4	44.7	56.7
Daylight period in midwinter = 475 min;	Mean available for feeding on spring tides = 475 x 0.7 = 333; on neap = 475 x 0.95= 451			
Energy required/min (cal) neap - spring	26.6 - 36.0	40.8 - 55.3	99.1 - 134.2	125.7 - 170.3
No. of ¼ bill-height worms required/min	4.1 - 5.6	6.3 - 8.6	13.5 - 18.3	17.1 - 23.2
No. of small Crustacea required/min	12.1 - 16.4	18.6 - 25.1		

Sources: [1]Evans & Smith (1975), Pienkowski *et al.* (1979), N.C. Davidson (pers. comm.)
[2]Based on Lasiewski & Dawson (1967)
[3]Smith (1975), Evans *et al.* (1979); Paper 1

acquiring 2/3 of their total intake at night. The hours per day available for feeding in spring in spring and neap tidal situations differ and are based on the data for plovers in Figure 8 of Paper 1. This assessment of potential feeding time may be a slight over-estimate for the sandpipers (see Smith 1975). Required calorific intakes per minute can then be calculated (Table 23). Estimations of worm length indicated that at low temperatures the mean sizes of worms taken by both plover species were about $\frac{1}{4}$ x bill-height. The average calorific values of such worms were, respectively, 6.45 cal for Ringed Plovers (this figure is used also for Dunlins) and 7.34 cal for Grey Plovers(used also for Godwits) (Paper 1). Thus the energy requirements can be expressed in terms of numbers of $\frac{1}{4}$ bill-height worm units per minute (Table 23). For the two smaller waders, the numbers of small Crustacea equivalent to the required calorific intakes are also given in Table 23, based on 2.2 cal/animal (Paper 1).

Several studies have indicated that waders can buffer short-term shortages of resources by depositing fat and protein reserves (Evans & Smith 1975, Dick & Pienkowski 1979, Pienkowski *et al.* 1979, Davidson 1979). Thus, on the assumption that a small surplus food intake during neap tides buffers a small deficit during spring tides, mean spring/neap values of requirements are used below and in Figures 24 & 25.

Figure 24 shows the requirement levels in terms of $\frac{1}{4}$ bill-height worms for Grey Plovers and Godwits. Also shown are the estimated numbers of outflows per minute within a Grey Plover's search area in relation to density of worms for several different temperatures. These estimates are obtained from the mean of Figures 3 (a) & (b). Also shown are the estimated number of thin worms detectable per minute by Godwits. This is based on a search area of 9 m^2 per minute (Smith 1975), 50% of worms within detectable depth (Smith 1975, present paper) and 1% of such worms in this search area being detectable and catchable by godwits. This last value is a maximum justified by Pienkowski (1980); in an examination of Smith's (1975) results, the proportion detected and catchable did not reach this figure even when the godwits were clearly feeding on thin worms as fast as they could. Figure 26 summarizes the data on estimated minimum acceptable prey densities in Figure 24.

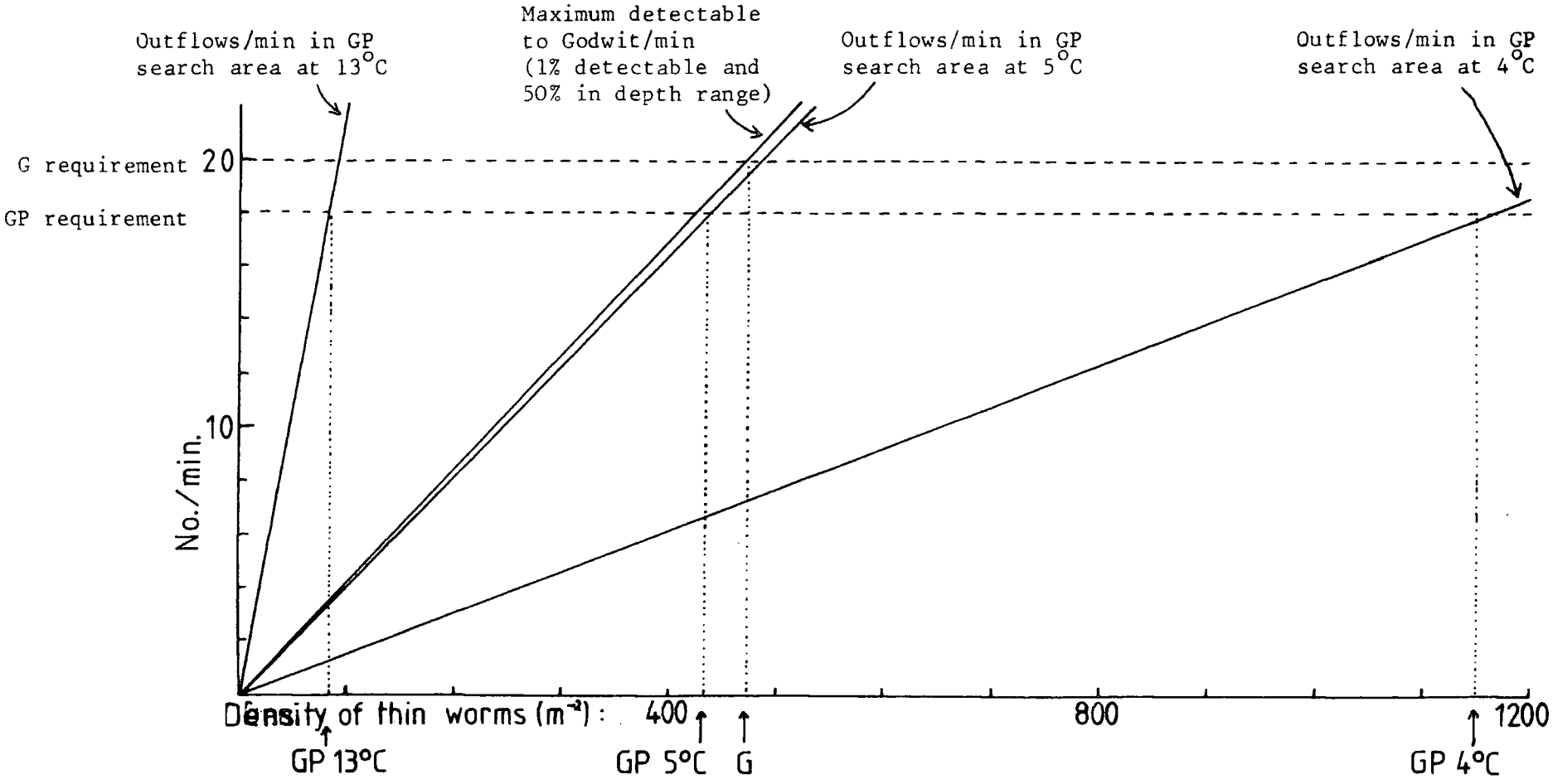


Figure 24. Model of minimum required feeding rates of Grey Plovers (GP) and Bar-tailed Godwits (G) on thin worms and availability of these in relation to prey density and sand temperature. ———numbers of available prey in search area; – – – –minimum intake rate required; ·····minimum acceptable prey density at given temperature for given species.

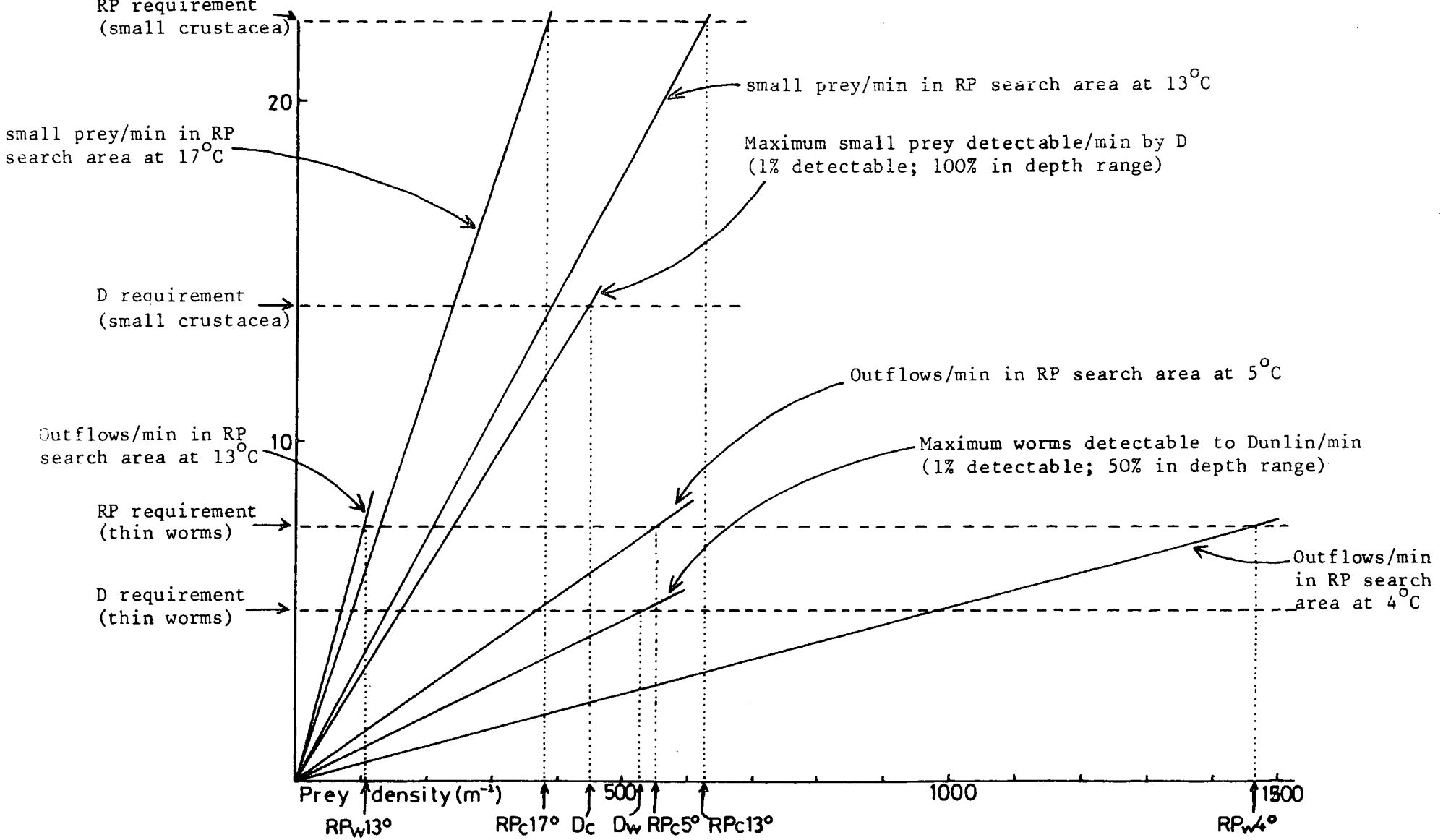


Figure 25. Model of minimum required feeding rates of Ringed Plovers (RP) and Dunlins (D) and availability of prey in relation to prey density and sand temperature. ——— no. of available prey in search area; - - - - - - minimum intake rate required; ····· minimum acceptable prey density of worms (w) or crustacea (c) at given temperature for given species.

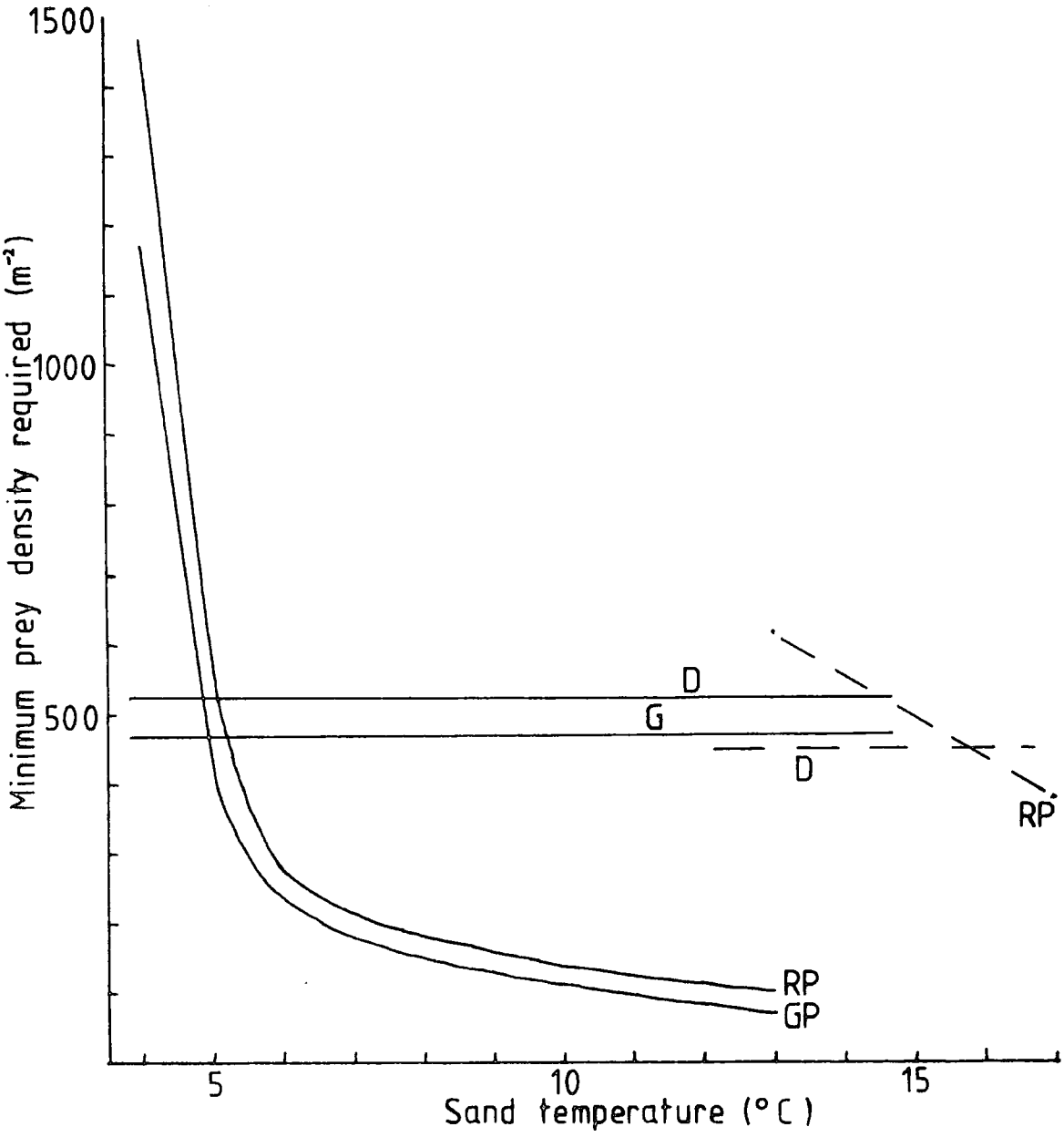


Figure 26. Model of minimum acceptable prey densities for various shorebirds on Holy Island Sands in relation to temperature. Based on Figures 24 & 25

——— Estimated minimum acceptable densities of thin worms (mainly *Notomastus*) for Ringed Plover (RP), Dunlin (D) and Bar-tailed Godwit (G)

— — — Estimated minimum acceptable densities of small crustacea.

Variation in energetic requirements with temperature not included. Dunlin and Bar-tailed Godwit should show some temperature effects because of variations of depth distribution and detectability with temperature but these are far smaller than the variations in surface activities relevant to plover foraging.

It is clear from Figures 24 & 26 that at low temperatures, because of low prey availability, Grey Plovers require to feed in areas of high densities of prey. (Indeed, the situation of the birds is probably even worse as Figure 24 ignores the higher energy requirements of birds at lower temperatures.) At $4^{o}C$ (at which temperature very few *Arenicola* are taken) a minimum density of about 1200 thin worms/m^2 is required. As can be seen from Figures 2 & 3 of Paper 1, such densities are restricted to a few small areas at Lindisfarne and this may account for the relatively large flocks on these (the main study areas) in adverse conditions. Tactile foraging Godwits can utilize lower densities of worms at such temperatures but, because worm depth is less sensitive to temperature than worm activity, a rise in temperature has less effect on the feeding rates on thin worms by godwits than by plovers even if all worms come within depth reach (as indicated in Figure 24). At high temperatures, Grey Plovers can utilize much lower densities than godwits but, of course, other prey may also be available then. The presence of any food such as *Arenicola* which gives a high net energy intake per unit time allows lower acceptable densities of alternative prey (thin worms) for the rest of the available feeding time.

Arenicola differ from thin worms in that when lying in the galleries of their burrows they are out of reach of godwits. If they are within reach, they are also moving to or from the surface. In such a situation any worm available to a tactile forager is usually available (albeit for a shorter time) also to a visual forager which has the advantage of longer detection range. Thus both Godwits and Grey Plovers use visual searching while feeding on these. Although Godwits appear to be able to feed at high density and to exclude Grey Plovers the tide edge, it is possible that the plovers' higher speed of movement makes them better able to exploit the lower frequency of activity of *Arenicola* above the tide edge than are the godwits.

Figures 25 and 26 presents similar data on Ringed Plovers and Dunlins. The data on Dunlin search area of 3.2 m^2/min, and estimates of detectability and catchability factors similar to those of Godwit were based on examination of ciné-film of Dunlins feeding in the same area as Ringed Plovers. At low temperatures, Ringed Plovers require similarly high densities of worms as Grey Plovers, but Dunlins are able

to utilize much lower densities. In increasingly warm conditions, Ringed Plovers are able to exploit progressively lower densities of prey. This is important on the High Flats where Ringed Plovers are able to exploit a lower density of the (low-density) surface-living Crustacea than could be used by a Dunlin foraging mainly by touch. In fact, on the High Flats, Dunlins normally fed by a largely visual method.

Dunlins were also seen to feed by a plover-like stop-run-peck technique on several occasions at night at Lindisfarne, usually when there was some moonlight (pers. obs.). On two occasions a similar unexpected stop-run-peck feeding method was observed, only at night, in Redshank at Teesmouth in a site receiving some illumination from road lamps (Pienkowski 1973). For Dunlin and Redshank, which usually feed chiefly by touch, this change to apparently visual feeding at night when the range of vision is presumably less than by day (see above for evidence of this in plovers) seemed anomalous. Presumably, the reason for the change was the increased surface activity at night of various prey discussed above. With some light from the moon or street lamps, the sandpipers were presumably able to exploit the change of prey behaviour in a few situations.

The tactile foraging sandpipers thus appear to be better adapted to colder climates than are plovers although the latter manage to survive by building up large energy reserves in autumn (Pienkowski 1980, Davidson 1979). The plovers are, however, better adapted to warmer areas where they can exploit lower densities of available prey than can sandpipers. This is reflected in the distributions of the two types of species in the non-breeding seasons (Pienkowski 1980). Plovers tend to occur at lower latitudes, where in winter the longer daylight period in every 24 hours will also be to their advantage.

SUMMARY

The effects of environmental conditions on the foraging behaviour of Ringed and Grey Plovers and the behaviour of their prey were investigated at Lindisfarne National Nature Reserve, Northumberland. Plovers forage by an apparently visual searching technique, scanning an area while standing still before running to peck at prey.

The intertidal invertebrates *Arenicola*, *Notomastus*, *Bathyporeia* and *Eurydice* increased their surface activity in relation to variations in environmental conditions, particularly warmer temperatures. The plovers detected and caught prey by exploiting the brief periods of surface activity. As prey became more available, the numbers of prey taken per minute increased at first, but at higher temperatures, rates of capture of smaller prey decreased as larger items were selected. When activity of surface-living small Crustacea was low, Ringed Plovers used foot-vibration to stimulate movement of these animals, making them visible.

A simple model to describe the foraging behaviour of plovers is proposed. Plovers appeared to select large prey in suitable conditions by being less responsive to cues of small prey at the start of each waiting period but progressively became more ready to take smaller prey before eventually giving-up and moving to a new waiting site. The birds tended to concentrate their activity on clumps of high density of available prey by moving less far after taking large prey than small or no prey. When no prey was taken after a wait, the bird moved on sufficiently far to scan a new area, or farther in areas of low density, highly clumped prey.

The plovers tended to feed as close to each other as compatible without interfering with each other's foraging and gathered together on the areas of highest prey density when adverse environmental conditions caused lowest prey availability. An attempt is made to predict the minimum densities of prey required for energy balance in various conditions and to compare the foraging strategies of visually-foraging plovers and tactilely-foraging sandpipers. The presence of other shore-birds foraging tactilely and thereby tolerant of high densities,

caused plovers to move to other (less favourable) feeding areas.

In addition to feeding by day, plovers also forage at night, and this is discussed in relation to visual foraging and the increased activity of some intertidal invertebrates at night.

REFERENCES

Bailey, N.T.J. 1959. *Statistical Methods in Biology*. English Univ. Press, London.

Baker, M.C. 1974. Foraging behavior of Black-bellied Plovers (*Pluvialis squatarola*). *Ecology* 55: 162-167

Baker, M.C. & Baker, A.E.M. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monog.* 43: 193-212

Bolze, G. 1968. Nordung und Bau der Herbstschen Körperchen in Limicolenschnäbeln im Zusammenhang mit der Nahrungsfindung. *Zoologischer Anzeiger* 181: 311-355.

Brady, F. 1943. The distribution of the fauna of some intertidal sands and muds on the Northumberland coast. *J.Anim.Ecol.* 12: 27-41

Buchsbaum, R. 1951. *Animals without backbones*. 2 vols. Pelican, London

Burton, P.J.K. 1974. *Feeding and the Feeding Apparatus in Waders*. Brit. Mus. (Nat. Hist.), London

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theor.Popul.Biol.* 9: 129-136

Davidson, N.C. 1979. Changes in the body composition of shorebirds during winter. *Wader Study Group Bull.* 26: 29-30

Davies, N.B. 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*) in a field study on optimal foraging. *Anim.Behav.* 25: 1016-1033

Davis, J.M. 1975. Socially induced flight reactions in pigeons. *Anim.Behav.* 23: 597-601

Dick, W.J.A. & Pienkowski, M.W. 1979. Autumn and early winter weights of waders in north-west Africa. *Ornis Scand.* 10: 117-123

Drinnan, R.E. 1958. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the Edible Mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. *Fishery Invest., London* Ser 2 22(4): 1-15

Dugan, P.J., Evans, P.R., Goodyer, L.R. & Davidson, N.C. in press. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. *Ibis*

Eltringham, S.K. 1971. *Life in Mud and Sand* English Univ. Press, London

Emlen, J.M. 1966. The role of time and energy in food preference. *Amer.Nat.* 100: 611-617

Enright, J.T. 1962. Responses of an amphipod to pressure changes. *Comp.Biochem.Physiol.* 7: 131-145

Enright, J.T. 1965. Entrainment of a tidal rhythm. *Science* 147: 864-867

Evans, P.R. 1975. Notes on the feeding of waders on Heron Island. *Sunbird* 6: 25-30

Evans, P.R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea* 64: 117-139

Evans, P.R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal prey. pp 357-366 in E. Naylor & R.G. Hartnoll (Eds.) *Cyclic phenomena in marine plants and animals.* Pergamon, Oxford & New York

Evans, P.R. & Smith, P.C. 1975. Studies on shorebirds at Lindisfarne, Northumberland. 2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. *Wildfowl* 26: 64-76

Fallet, M. 1962. Über Bodenvögel und ihre terricolen Beutetiere. Technik der Nahrungssuche - Populations dynamik. *Zool.Anz.* 168: 187-212

Fincham, A.A. 1970a. Amphipods in the surf plankton. *J.mar.biol.Ass. U.K.* 50: 177-198

Fincham, A.A. 1970b. Rhythmic behaviour of the intertidal amphipod *Bathyporeia pelagica.* *J.mar.biol.Ass. U.K.* 50: 1057-1068

Geppetti, L. & Tongiorgi, P. 1967. Nocturnal migrations of *Talitrus saltator* (Montagu) (Crustacea Amphipoda). *Monitore Zool. Ital. (N.S.)* 1: 37-40.

Goss-Custard, J.D. 1969. The winter feeding ecology of the Redshank *Tringa totanus.* *Ibis* 111: 338-356

Goss-Custard, J.D. 1970a. Dispersion in some overwintering wading birds. pp 3-35 in J.H. Crook (Ed.). *Social behaviour in birds and mammals.* Academic Press, London

Goss-Custard, J.D. 1970b. The responses of Redshank (*Tringa totanus* (L.)) to spatial variation in the density of their prey. *J.Anim.Ecol.* 39: 91-113

Goss-Custard, J.D. 1970c. Factors affecting the diet and feeding rate of the Redshank (*Tringa totanus*). pp 101-110 in A. Watson (Ed.) *Animal populations in relation to their food resources.* Blackwell, Oxford & Edinburgh

Goss-Custard, J.D. 1976. Variation in the dispersion of Redshank *Tringa totanus* on their winter feeding grounds. *Ibis* 118: 257-263

Goss-Custard, J.D. 1977a. The energetics of prey selection by Redshank, *Tringa totanus* (L.), in relation to prey density. *J.Anim. Ecol.* 46: 1-19

Goss-Custard, J.D. 1977b. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *J.appl.Ecol.* 14: 721-739

Goss-Custard, J.D. 1977c. Optimal foraging and the size selection of worms by Redshank, *Tringa totanus*, in the field. *Anim. Behav.* 25: 10-29

Goss-Custard, J.D. 1977d. Predator responses and prey mortality in Redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *J.Anim.Ecol.* 46: 21-35

Goss-Custard, J.D. 1978. Sequential choice for prey size by captive Redshank *Tringa totanus*. *Ibis* 120: 230-232

Goss-Custard, J.D., Evans, P.R., Knights, P.J. & Pienkowski, M.W. in prep. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. 2. Changes in feeding ecology and foraging behaviour.

Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newbery, P.E. & Williams, R. le B. 1977. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (Charadrii). *J.appl.Ecol.* 14: 701-719

Green, J. 1968. *The Biology of Estuarine Animals.* Sidgwick & Jackson, London

Hamilton, W. 1971. Geometry for the selfish herd. *J.theor.Biol.* 31: 295-311

Heppleston, P.B. 1971. The feeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland. *J.Anim.Ecol.* 40: 651-672

Heppner, F. 1965. Sensory mechanisms and environmental clues used by the American Robin in locating earthworms. *Condor* 67: 247-256

Hulscher, J.B. 1976. Localisation of cockles (*Cardium edule* L.) by the oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea* 64: 292-310

Jansson, B.O. & Kallander, C. 1968. On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea. *J.exp. mar.Biol. Ecol.*2: 24-36

Jones, D.A. & Naylor, E. 1970. The swimming rhythm of the sandbeach isopod *Eurydice pulchra*. *J.exp.mar.Biol.Ecol.*4: 188-199

Kitching, J.A. & Ebling, F.J. 1967. Ecological studies at Lough Ine. *Adv.Ecol.Res.* 4: 197-291

Krebs, J.R. 1973. Behavioural aspects of predation. pp 73-111 in P.P.G. Bateson & P.H. Klopfar (Eds.) *Perspectives in Ethology.* Plenum Press, New York

Krebs, J.R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). *Behaviour* 51: 99-134

Krebs, J.R. & Cowie, R.J. 1976. Foraging strategies in birds. *Ardea* 64: 98-116

Krebs, J.R., MacRoberts, M.H. & Cullen, J.M. 1972. Flocking and feeding in the Great Tit *Parus major* - an experimental study. *Ibis* 114: 507-530

Krebs, J.R. & Partridge, B. 1973. The significance of head tilting in the great blue heron. *Nature* 242: 533-534

Krebs, J.R., Ryan, J.C. & Charnov, E.L. 1974. Hunting by expectation or optimal foraging? A study of patch use by Chickadees. *Anim.Behav.* 22: 953-964

Lange, G. 1968. Uber Nahrung, Nahrungsaufnahme und Verdsuungstrakt mitteleuropaischer Limikolen. *Beitr.Vogelkunde* 13: 225-334

Lasiewski, R.C. & Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 12-23

Lazarus, J. 1972. Natural selection and the functions of flocking in birds: a reply to Murton. *Ibis* 114: 556-558

Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim.Behav.* 27: 855-865

Little, C. & Nix, W. 1976. The burrowing and floating behaviour of the gastropod *Hydrobia ulvae*. *Estuarine Coastal Marine Sci.* 4: 537-543

MacArthur, R.H. & Pianka, E.R. 1966. On the optimal use of a patchy environment. *Amer.Nat.* 100: 603-609

Milne, H. & Dunnet, G.M. 1972. Standing crop, productivity and trophic relations of the fauna of the Ythan Estuary. pp. 86-106 in R.S.K. Barnes & J. Green (Eds.). *The Estuarine Environment.* Applied Science Publishers, London

Morgan, E. 1965. The activity rhythm of the amphipod *Corophium volutator* Pallas and its possible relationship to changes in hydrostatic pressure associated with the tides. *J.Anim.Ecol.* 34: 731-746

Murton, R.K. 1971a. Why do some bird species feed in flocks? *Ibis* 113: 534-536

Murton, R.K. 1971b. The significance of a specific search image in the feeding behaviour of the wood pigeon. *Behaviour* 39: 10-42

Naylor, E. 1958. Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *J.exp.Biol.* 35: 602-610

Naylor, E. 1962. Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. *J.Anim.Ecol.* 31: 601-609

Naylor, E. 1963. Temperature relationships of the locomotor rhythm of *Carcinus*. *J.exp.Biol.* 40: 669-679

Newell, R.C. 1962. Behavioural aspects of the ecology of *Peringia* (= *Hydrobia*)*ulvae* (Pennant). *Proc.zool.Soc. London* 138: 49-75

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. 1975. *SPSS: Statistical package for the social sciences.* 2nd ed. McGraw-Hill, New York

O'Connor, R.J. & Brown, R.A. 1977. Prey depletion and foraging strategy in the Oystercatcher *Haematopus ostralegus*. *Oecologia* 27: 75-92

Owens, N.W. & Goss-Custard, J.D. 1976. The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. *Evolution* 30: 397-398

Page, G. & Whitacre, D.F. 1975. Raptor predation on wintering shorebirds. *Condor* 77: 73-83

Palluault, M. 1954. Notes écologiques sur le *Talitrus saltator* L. *Arch. Zool. expérimentale et générale. Notes et Revue.* 91: 105-129

Perry, R. 1945. *A Naturalist on Lindisfarne.* Country Life, London

Pienkowski, M.W. 1973. Feeding activities of wading birds and Shelducks at Teesmouth and some possible effects of further loss of habitat. Report to Coastal Ecology Research Station, Inst. of Terrestrial Ecology (formerly the Nature Conservancy).

Pienkowski, M.W. 1980. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. *Proc. IWRB Feeding Ecology Symp., Gwatt, Switzerland, Sept. 1977. Verh.Orn.Ges.Bayern* 23: in press

Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26: 134-148

Preece, G.S. 1971. The swimming rhythm of *Bathyporeia pilosa* (Crustacea: Amphipoda). *J.mar.biol.Ass. U.K.* 51: 777-791

Pulliam, H.R. 1973. On the advantages of flocking. *J. theor.Biol.* 38: 419-422

Pulliam, H.R. 1974. On the theory of optimal diets. *Amer.Nat.* 108: 59-74

Reading, C.J. & McGrorty, S. 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. *Estuarine Coastal Marine Sci.* 6: 135-144

Schoener, T.W. 1971. Theory of feeding strategies. *Ann.Rev.Ecol. Syst.* 2: 369-404

Simmons, K.E.L. 1961. Foot-movements in plovers and other birds. *Brit. Birds* 54: 34-39

Smith, J.N.M. 1975. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. *Behaviour* 49: 1-61

Smith, P.C. 1975. A study of the winter feeding ecology and behaviour of the Bar-tailed Godwit (*Limosa lapponica*). Unpublished Ph.D. thesis, University of Durham

Smith, P.C. & Evans, P.R. 1973. Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. *Wildfowl* 24: 135-139

Sokal, R.R. & Rohlf, F.J. 1969. *Biometry*. Freeman, San Francisco

Sparks, J.H. 1961. The relationship between foot-movements and feeding in shorebirds. *Brit. Birds* 54: 337-340

Swennen, C. 1971. Het voedsel van de Groenpootruiter *Tringa nebularia* tijdens het nerblijf in het Nederlandse Waddengebied. *Limosa* 44: 71-83

Swennen, C. & van der Baan, G. 1959. Tracking birds on tidal flats and beaches. *Brit. Birds* 52: 15-18

Thomson, A.L. (Ed.) 1964. *A New Dictionary of Birds*. Nelson, London

Trevor, J.H. 1978. The dynamics and mechanical energy expenditure of the polychaetes *Nephtys cirrosa*, *Nereis diversicolor* and *Arenicola marina* during burrowing. *Estuarine Coastal Mar Sci.* 6: 605-619

Vader, W.J.M. 1964. A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Neth.J. Sea Res.* 2: 189-222

Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *J.theor.Biol.* 30: 405-422

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information-centres' for food finding. *Ibis* 115: 517-534

Whittaker, R.H. 1970. *Communities and Ecosystems*. Macmillan, London

Zwarts, L. 1974. *Vogels van het brakke getijgebied, ecologische onderzoekingen op de ventsagerplaten*. Amsterdam

Zwarts, L. 1976. Density-related processes in feeding dispersion and feeding activity of Teal (*Anas crecca*). *Ardea* 64: 192-209

Paper 3. Development of feeding and foraging behaviours in young Ringed Plovers *Charadrius hiaticula*, and their relationship to growth and survival to reproductive age

INTRODUCTION

Shorebirds have become popular subjects for study in recent years, partly because of the increasing threats to their wintering areas and partly because of their convenience for observation while feeding on relatively simple prey communities. Unfortunately for such studies, in the breeding season most species become highly cryptic, particularly near the nest and with young. Observations on the behaviour and feeding (and even presence) of the latter are generally difficult to obtain (e.g. Holmes 1966, Harris 1967, Lack 1968, Nettleship 1973, Prater 1974, Ratcliffe 1976, Soikelli 1970b). Detailed studies are lacking, except for the Oystercatcher *Haematopus ostralegus* which is atypical of waders in that adults feed the young (Buxton 1939, Tinbergen & Norton-Griffiths 1964, Lind 1965, Norton-Griffiths 1967, Heppleston 1972).

Ringed Plovers breed in one of the most open habitats, incorporating much bare ground of sand or gravel, and are thus one of the most practicable species for study in the breeding season. This paper reports studies on the behaviour, feeding, growth and survival of young Ringed Plovers in the northern part of their range in NE Greenland in 1974 and near the southern limits at Lindisfarne, Northumberland in 1973 to 1976. The study at Lindisfarne also continues to consider post-fledging and later survival, dispersal, and recruitment.

The aim of this study was to investigate feeding and foraging behaviour of chicks in relation to age, area, season and environmental conditions and to see how changes in these affected growth rates and survival. It will be shown that in each main study area growth rates were remarkably similar in a wide range of situations and that feeding conditions did not normally affect growth or survival of Ringed Plover chicks at high or low latitudes. It is also concluded, however, that feeding ability may become important in late autumn on the wintering grounds.

STUDY AREAS

Scoresby Land

Observations were made near Mestersvig Government Station, Scoresby Land, NE Greenland (72°14' N, 23°55' W) during the Joint Biological Expedition to North East Greenland 1974. We were present in the area from 25 June to 16 August. The first young hatched on 24 July and the first fledged just before our departure. Some additional, less detailed, observations obtained by other members of the Expedition in other valleys in Scoresby Land (where times of the breeding season differed - Green, Greenwood & Lloyd 1977) are also incorporated.

The detailed study area around Mestersvig station (Figs. 1, 2) was mainly 'river-bed' shingle and sparse tundra heath (i.e. 30-60% covered by vascular plants; organic crust of lichen covering ground between heath plants; some disturbance by frost heaving - see Green *et al.* 1978, Green 1978a). During the study period, snow cover decreased progressively from greater than 90% on 25 June to about 60% on 6 July and to less than 10% by late July. Generally a damp zone was formed in tha latest areas from which snow had melted and also in small pools and streams. The shore of the small inlet, Noret, was ice covered until mid-July, after which melt run off and slight tidal movement gave rise to another damp zone there. Some of the other areas visited in NE Greenland had more vegetation cover but Ringed Plovers tended to occupy the more barren areas (see Green 1978a, Ferns 1978a).

Northumberland

Studies at Lindisfarne National Nature Reserve (55°40' N, 1°50' W) and adjacent parts of the Northumberland coast (Figs. 1 & 3) took place from 1973 to 1976. In 1973 only occasional visits were made to obtain information on distribution and to colour-ring the young. More detailed work was undertaken in early 1974 and throughout 1975 and 1976. After mid-June 1974, in my absence, young were colour-ringed by P.J. Knights.

At Lindisfarne the Ringed Plovers breed on or near the shore. Detailed studies took place mainly around Holy Island Snook where the habitat includes sandy and pebbly beaches and intertidal area. In other parts of the Reserve, some muddy areas were included, as well as

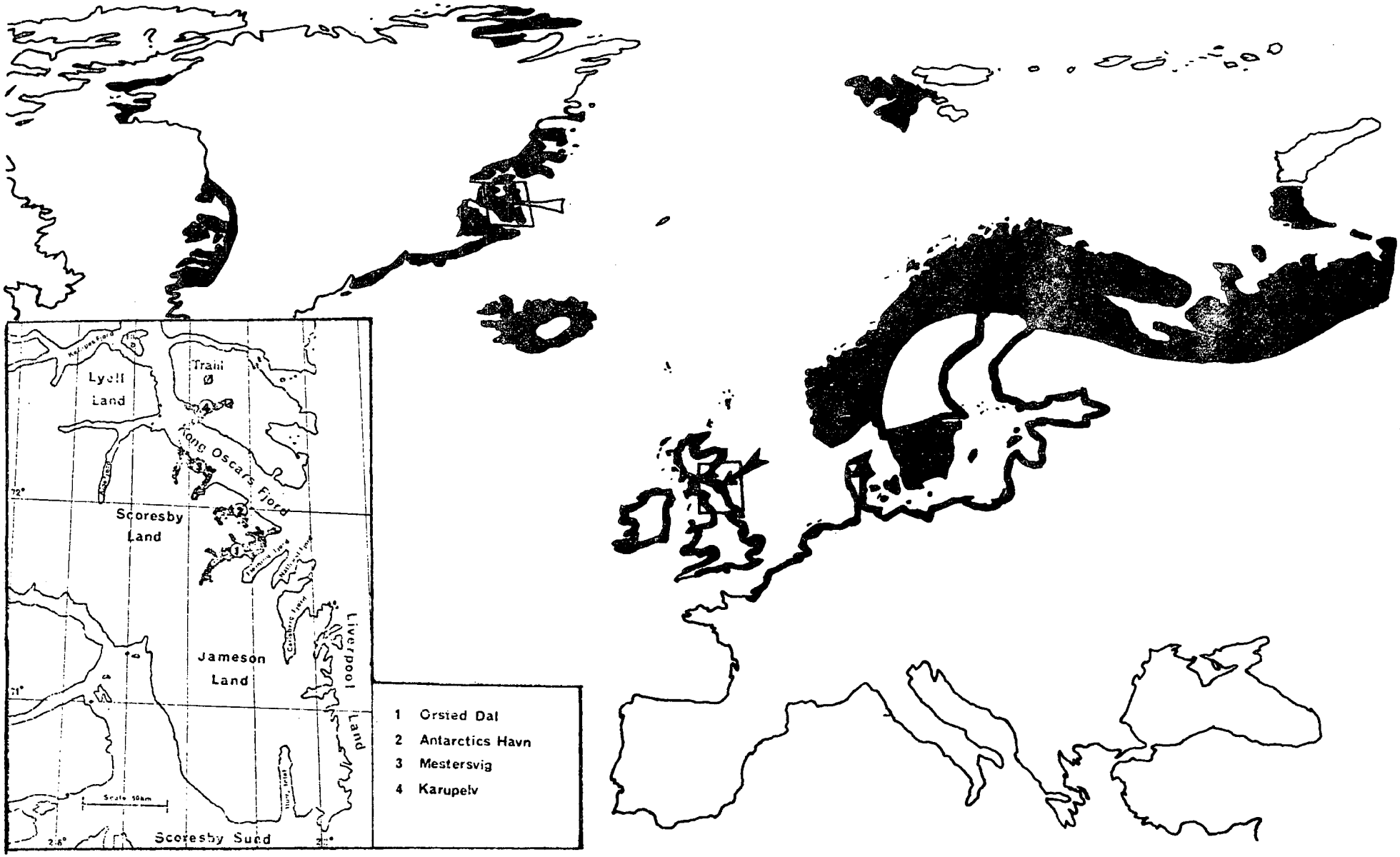


Figure 1. The western part of the breeding distribution of Ringed Plovers, according to Voous (1960). Location of main study sites indicated by arrows. Boxes indicate the wider study areas in Greenland (inset) and northern England and SE Scotland (Fig. 17).

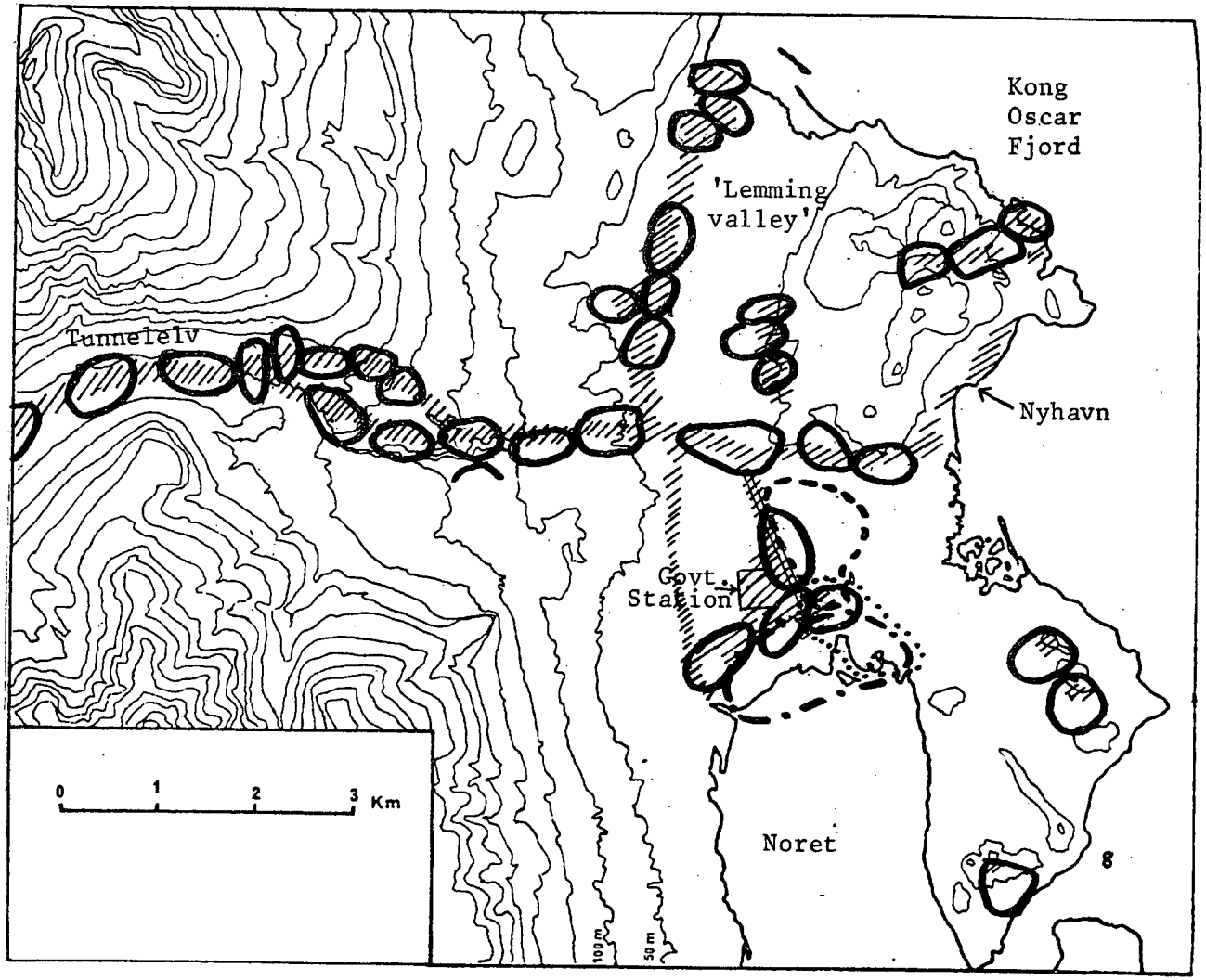


Figure 2. Study area at Mestersvig.

Areas with snow-free patches in late June (consisting mainly of cleared tracks and runway, some steeper slopes and river gravels).

Ringed Plover territories ; } limits of brood areas of three families watched

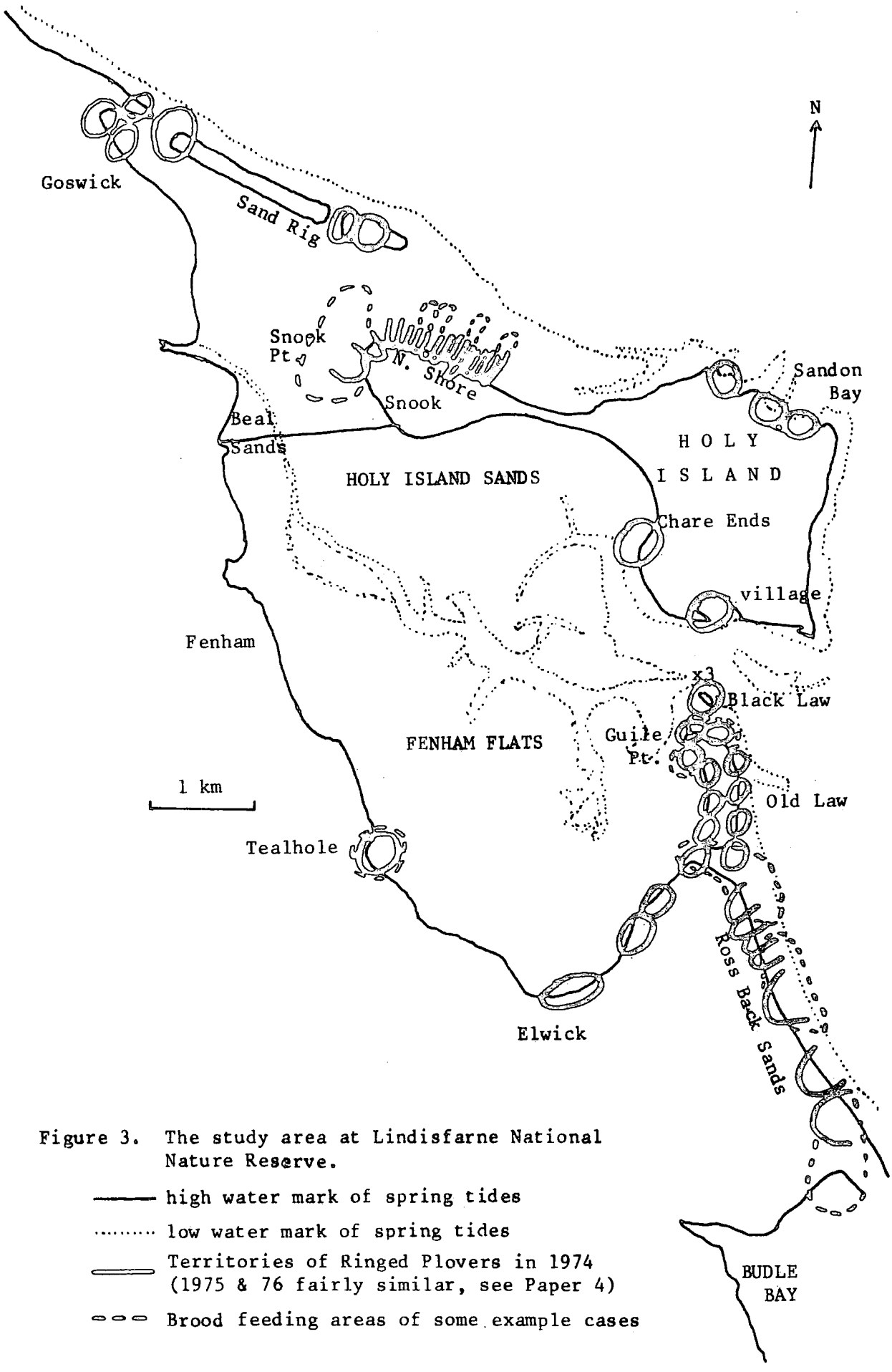


Figure 3. The study area at Lindisfarne National Nature Reserve.

——— high water mark of spring tides

..... low water mark of spring tides

═══ Territories of Ringed Plovers in 1974 (1975 & 76 fairly similar, see Paper 4)

⊂⊃⊂⊃⊂⊃ Brood feeding areas of some example cases

exposed sandy beaches with pronounced strand lines but little intertidal feeding area.

METHODS

Birds were watched using a tripod-mounted 15-60x telescope, at Lindisfarne usually from a hide on dunes adjacent to the shore or from a car, but at Mestersvig, where the plover family parties tended to range more widely, by an observer standing in the open and moving when necessary, but keeping sufficiently distant so as not to cause disturbance. In Greenland, family parties were usually watched for 24 h periods, 2400 to 0600 and 1200 to 1800 normally being covered by myself and 0600 to 1200 and 1800 to 2400 by another observer, usually D.I. North. Time of day is given as GMT (which is used locally, although solar midnight occurs at 0136). At this time of year the sun did not drop below the horizon although it was lower in the sky and in some situations hidden by hills around midnight and 'nights' tended to be considerably cooler than 'days' (see below). At Lindisfarne, only one observer was normally available and watches either covered the whole daylight period or different parts of this were covered on adjacent days. Although at this latitude in the summer the short nights are not very dark, it was not usually possible to watch family parties during the night, although some observations were made in 1976 using an image intensifier. Observations later in the night and early morning were particularly difficult to obtain because of the problems of locating the brood in the dark and poor light. Mist was fairly common in the early morning. (Some extra observations made by Miss S. Jones, Miss S. Parkinson, P. Snell, F.W. Purnell and Miss S. Dick conducting undergraduate projects under my direction are also utilised.) Times were recorded as British Summer (or Standard) Time, midnight occurring at about 0108, so that times in the two areas are roughly comparable. Observations were recorded either in a notebook or dictated into a tape-recorder and transcribed later.

Prey was identified where possible from visual observations and examination of potential prey types in the areas the birds were feeding: usually the possible range was very limited. Pecking rates in Greenland were measured using a stopwatch. The numbers of identifiable

items also being noted. In Northumberland, pecking rates were measured both by this method and by using a continuously running tape-recorder to record additionally times for each foraging behaviour and distances moved, as described in Paper 2. Checks of the reliability and validity of these methods of describing prey and foraging behaviour of adults and chicks were carried out using ciné-film as described in Papers 1 & 2 for adult birds, with similar results. On a chick aged about 1 week at least 89% of pecks resulted in an item being taken but suitable short-range ciné-film was not available for younger chicks.

During each observation period note was kept of weather conditions, including air temperature at ground level, wind force and direction and rainfall and, in Greenland, these were supplemented by records at the meterological station, which was within the study area.

At both study areas, as many chicks and adults as possible (generally including all families studied in detail) were marked with combinations of colour rings, unique to each individual. Later ringing and observations of ringed birds at Lindisfarne by P.A. Snell, P.R. Evans and L.R. Goodyer are also incorporated where appropriate. Chicks were weighed at capture and attempts were made to recapture them later (not more frequently than about 1 week between captures) to estimate rate of weight gain.

RESULTS

Dates of hatching, growth rates and fledging periods

The three broods studied in detail in NE Greenland hatched on 24-25, 27 and 28 July, this probably being fairly late for the area in general but not for the immediate Mestersvig area in 1974, a late season (see Green *et al.* 1977, and Fig. 4). Hatching dates at Lindisfarne in 1975 and 1976, the two years of full coverage throughout the season are given in Figure 5.

After hatching and drying Ringed Plovers are about 13% of adult weight, Greenlandic young being slightly smaller than Northumbrian ones in absolute terms but slightly larger relative to adult weight (Table 1). Weights remain constant or normally fall slightly during the first

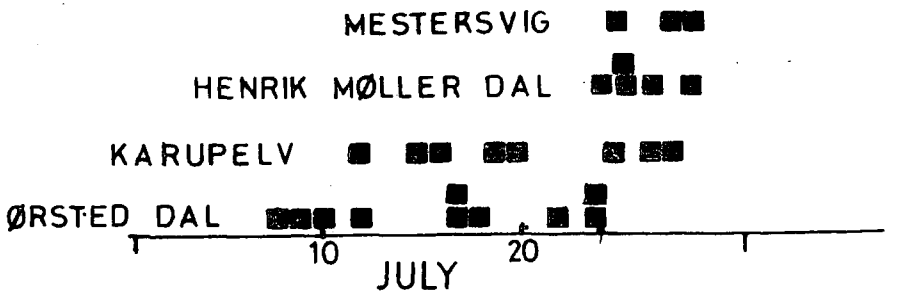


Figure 4. Hatching dates of Ringed Plovers in Scoresby Land in 1974.

(Some dates estimated from chick weights - see Green *et al.*1977). ■ = 1 nest

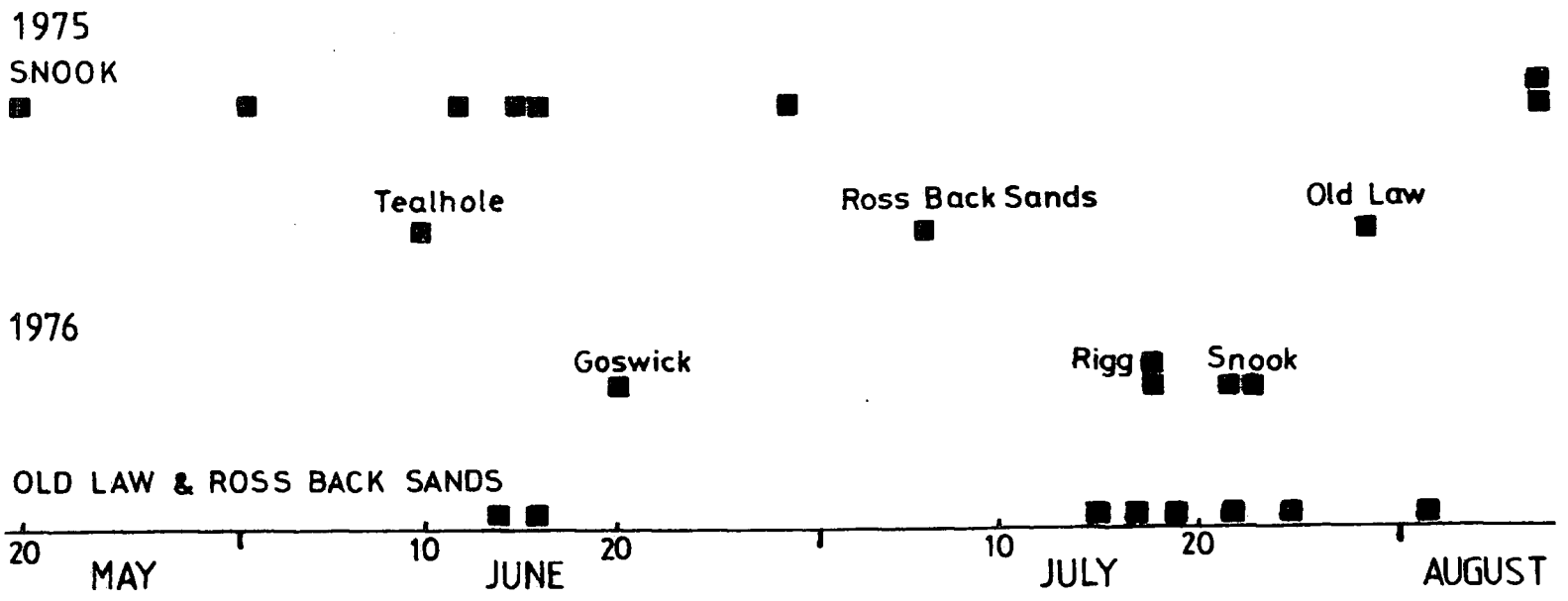


Figure 5. Hatching dates of Ringed Plovers at Lindisfarne.

(Ross Back Sands and Old Law were not fully covered in 1975). ■ = 1 nest

TABLE 1. MEAN WEIGHTS (g) OF RINGED PLOVERS IN NE ENGLAND AND NE GREENLAND

	LINDISFARNE			SCORESBY LAND		
	n	$\bar{x}$	s.e.	n	$\bar{x}$	s.e.
Breeding males	7	67.9	1.28	15	59.1	0.68
Breeding females	15	71.1	0.57	12	61.1	1.33
Young at hatching	24	8.5	0.23	27	8.0	0.09
Mean weight of hatching young as percentage of weights of adult:						
male		12.6%			13.6%	
female		12.0%			13.2%	

day (as documented for Dunlin *Calidris alpina* by Soikelli 1967), and then increase at a fairly steady rate of about 2.5 g/day from 2-3 days old throughout most of the pre-fledging period (Fig. 6). At Lindisfarne, from 3 days old onwards, weight is related to age by the regression equation:

Weight (g) = 1.5 + 2.49 x days (n = 35, r = 0.95, r^2 = 0.90).

If weights from day 0 are included, this becomes:

Weight (g) = 6.7 + 2.06 x days (n = 81, r = 0.95, r^2 = 0.91)

The smaller sample of 13 weights of birds at Mestersvig gives a fairly similar line:

Weight (g) = 7.6 + 1.92 x days (r = 0.97, r^2 = 0.95).

Growth rates at Lindisfarne can also be calculated from chicks caught more than once, including birds of both known and unknown age (Fig. 7). A regression of weight increase on time between captures for birds not caught in the first day after hatching gives:

Weight (g) = 2.0 + 1.77 x days (n = 22, r = 0.87, r^2 = 0.76).

Inclusion of birds caught soon after hatching changes this to:

Weight (g) = -0.6 + 1.93 x days (n = 35, r = 0.89, r^2 = 0.79),

the negative intercept resulting from the low weight increases in the first days after hatching. The general similarity of these growth rates calculated from retraps to those of birds of known age supports the indication of fairly linear growth rate throughout the pre-fledging period after the first few days. A few data on growth rates obtained from retraps in Cumbria by J. Sheldon (*in litt.*) also approximate to this rate (Fig. 7), as do some from N. Norway (Miss C.M. Lessells pers. comm.), Uist, Outer Hebrides (Wilson 1978 & *in litt.*) and mean weights at known ages in Estonia (Keskpaik *et al.* 1970).

As illustrated in Figure 8, there was no indication of a seasonal trend in growth rates which were very similar for all individuals in Greenland and in Britain in all years. Wilson (1978), working on the machair of South Uist, suggests that chicks hatched on grass grow more slowly than those on plough but, although the regression coefficients were 1.37 and 1.82 respectively, the difference was not statistically significant.

Dates of first flights for broods are also indicated in Figure 6.

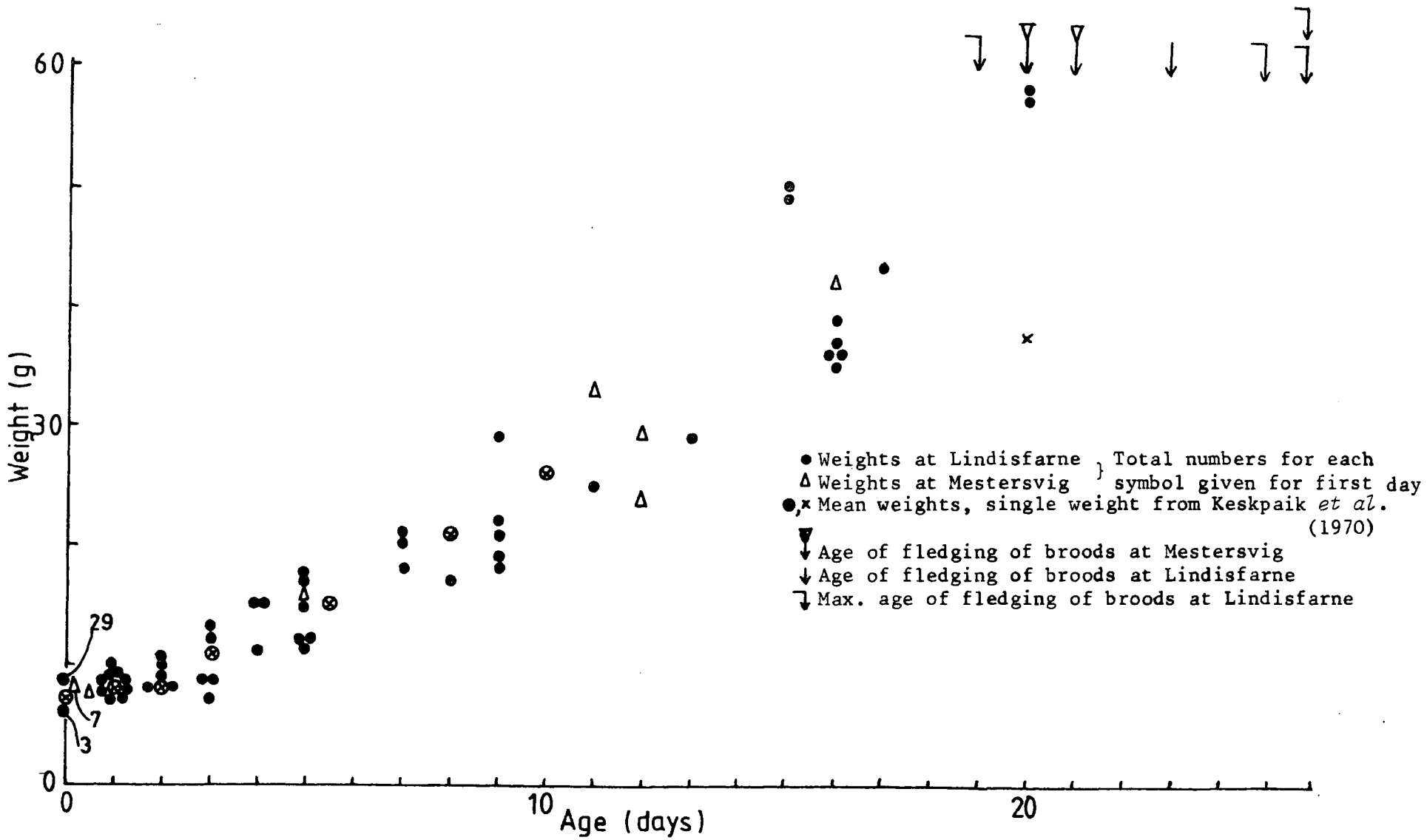


Figure 6. Weights and fledging in relation to age of chicks

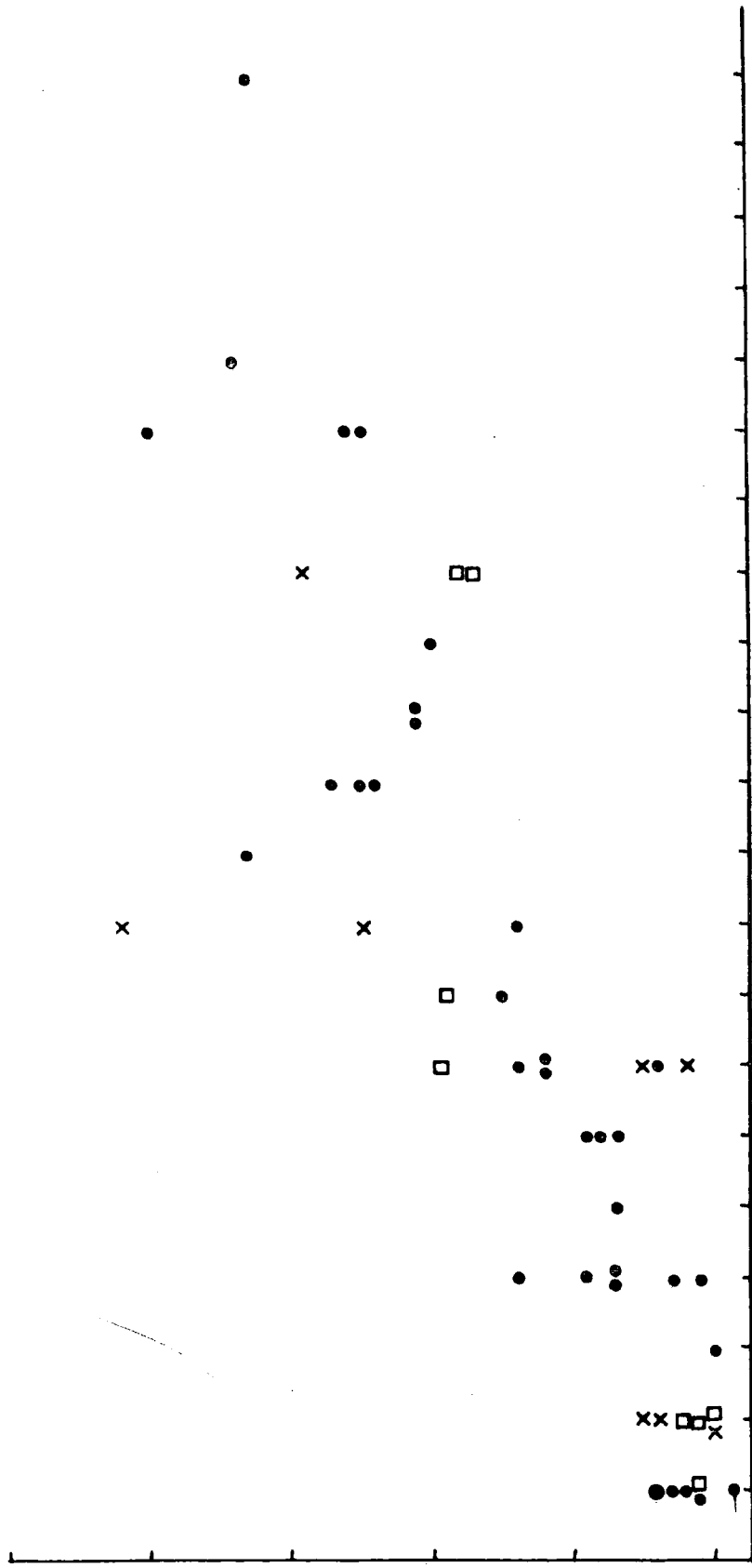


Figure 7. Weight increases of retrapped chicks

● Lindisfarne; × Cumbria (J. Sheldon, *in litt.*)

□ Varangerfjord, N. Norway (data of Oxford Expedition to Varangerfjord 1970, Miss C.M. Lessells *in litt.*)

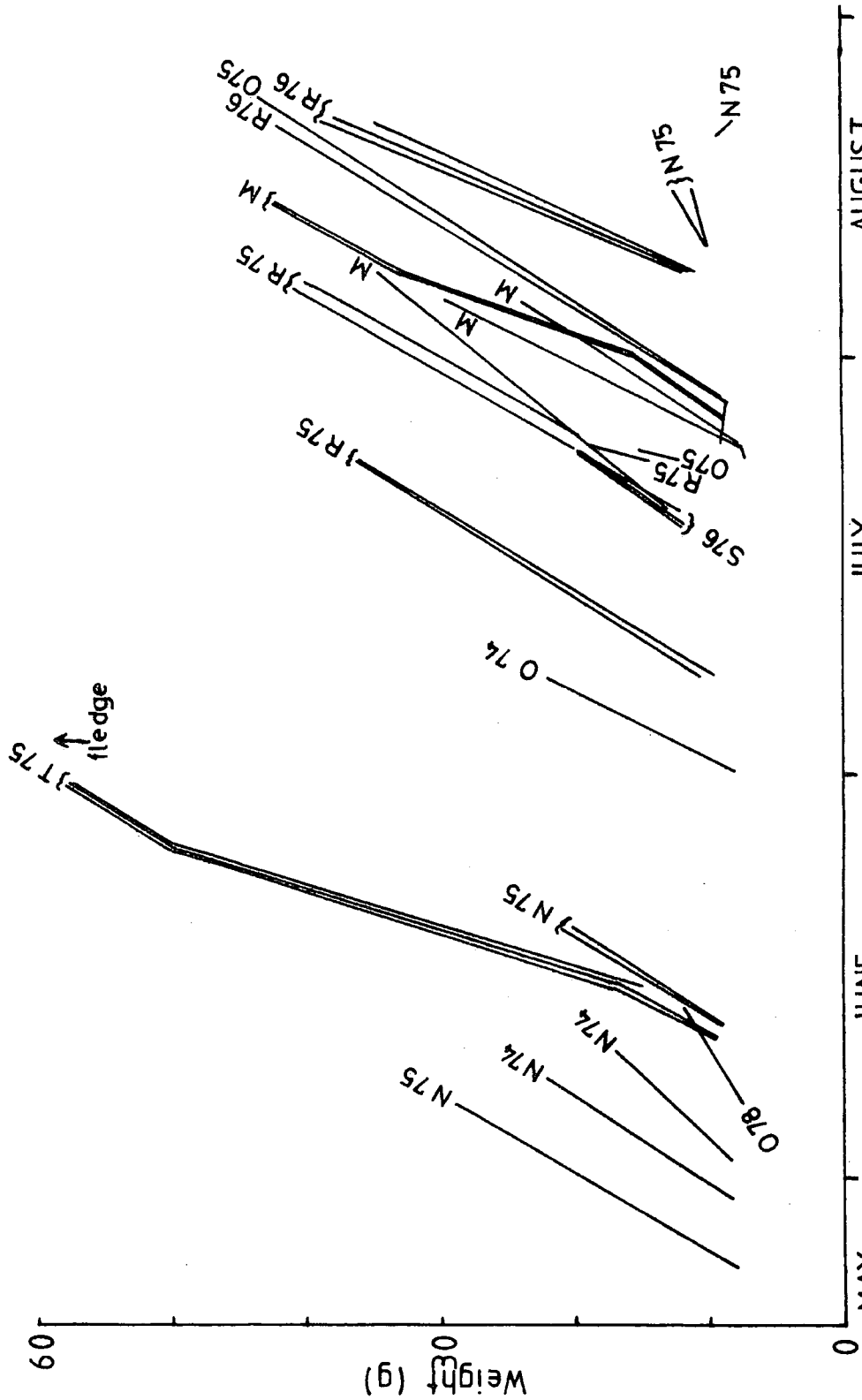


Figure 8. Weight changes of chicks in relation to season.

N = N. Shore; O = Old Law; R = Ross Back Sands; T = Tealhole; M = Mestersvig.

These were 20 and 21 days at Mestersvig and 19 (or less) and 23 days at Lindisfarne with some further maximum values of 25, 26 and 26 days at the latter site. These maximum figures arise from cases in which the chicks were suspected of being capable of flight for some time before this was observed. It seems that chicks may avoid flight (which is energetically expensive, presumably especially so if feathers are not fully grown and the bird inexperienced) even when capable of short flights unless there is a need to escape from a potential predator. Figure 6 suggests that fledging occurs at about 55-60 g. This coincides with the mean weight of juvenile Ringed Plovers caught at the Wash, E. England throughout the months July to September (McGregor & Jones 1979).

Detailed studies of the development of body organs were not made, although a few dead chicks were examined. Those parts of the body associated with self-feeding were large and well developed at hatching, these including legs, eyes, bill, gizzard, intestine and liver. Body plumage was already present and developed rapidly. Back plumage was cryptic and also apparently adapted to absorb radiant heat (Keskpaik *et al.* 1970). Flight feathers and pectoral muscles developed late, wing feathers (allowing fluttering escape flight) preceding tail feathers. This is as would be expected from the life style of the precocial self-feeding young and may be compared with the detailed studies of altricial passerines (e.g. O'Connor 1977).

Feeding areas and range

The feeding ranges of Ringed Plover broods at Mestersvig and Lindisfarne are shown in relation to earlier season territories in Figures 2 & 3. At the Snook and some other parts of the reserve at Lindisfarne, there was a tendency for broods to remain within territories, adjacent territories usually remaining occupied as other pairs made replacement or occasionally second nesting attempts during the long breeding season. Territorial behaviour was maintained in such situations. In some other parts of the reserve, notably the exposed sea beaches without rich intertidal feeding areas, the families often moved some way, especially after the young were a few days old.

At Mestersvig, territories broke down around hatching time and

those birds which had lost their nests did not attempt to renest (although some may have done so elsewhere in Scoresby Land where the season was earlier). Family parties ranged widely but avoided other family parties. The birds tended to move to damp areas, including the shore, although for many Ringed Plovers in this area, the shore is probably too far from the nesting area for this to be practicable.

Activity patterns

At both Mestersvig and Lindisfarne there was normally a spread of several hours between the hatching of first and last chicks. About half a day seemed typical but shorter and longer intervals were estimated. The brooding adult flew away with the larger egg shell fragments. After drying, chicks often left the nest scrape for short periods while the parent was off the nest but were usually recalled by the returning adult. Chicks were led from the nest within a few hours of hatching, one family party in Greenland moving 500 m in less than 24 h after hatching. In all three families watched in Greenland, the early hatching chicks left before the later ones so that the brood was divided into two or three groups for a time. Separation of chicks ranged from five to nearly 500 m. This clearly caused problems, as chicks only a few hours old required frequent brooding and could walk only a few metres between brooding periods. Similar behaviour was observed at Lindisfarne, except that the birds did not move very far, normally remaining in the small territories and near the nest.

The chicks began pecking almost as soon as they left the nest but at a very low rate (see below). Feeding behaviour, which developed rapidly, was mainly the run-stop-peck type of movement typical of plovers (see Paper 2) but during rapid feeding on abundant small prey, particularly in Greenland, the 'run' element was almost eliminated.

After the chicks left the nest scrape, the parents generally took turns to brood or be in immediate attendance on the chicks, brooding being shared fairly equally between male and female (Table 2). The possible lesser share of brooding by males at Lindisfarne may be due to the maintenance of territorial behaviour throughout the season here, as the male tended to perform more of this. The greater proportion of incubation by the male at Mestersvig may not be typical as most of the information comes from one family, which the female left shortly before

TABLE 2. SHARES OF BROODING BY THE TWO SEXES

Site/territory	Age of chicks (days)	Observed minutes of brooding by: ♂	♀	% of brooding by ♂
Mestersvig				
98MG004	7	252	377	43
98MG004	9	357	95	79
98MG004	11	140	70	76
98MG003	10	286	78	79
98MG004	17	89	0	100
Lindisfarne				
N Shore G 1974	1	115	149	44
N Shore G 1974	5	185	338	35
N Shore H 1975	2	106	169	39
Snook End 1976	10	142	137	51

The figures on any particular day may be biased by the timing of the observations in relation to the shifts of the birds and because the sex of the brooding bird could not always be determined.

the young fledged. The 'off-duty' bird fed, rested or 'stood guard' some distance away but within sight of the brood (usually less than 100 m). It was usually the first of the pair to give alarm calls and distraction displays when potential predators approached. The adults fed mostly when 'off-duty', rather than when attending the chicks. In a few cases both in Greenland and Northumberland one or other parent (of either sex) left the brood a few days before fledging (but well after the end of the period in which brooding occurs frequently - see below).

At Mestersvig, each pair made only one nesting attempt, territories breaking down early and failed birds leaving well before those with young. Some failed birds at Mestersvig remained in the area for a few days before leaving. Although they were seen to try to brood chicks of other pairs they were usually driven off, except when all the birds mobbed or distracted potential predators. Young were seen to be brooded by an adult other than the parents on one occasion: the 'adoption' was only temporary, lasting a few minutes.

At Lindisfarne, after fledging young birds moved around the area of the reserve and joined the early autumn flocks. The Mestersvig broods were watched only until about fledging. However, numerous juveniles from other areas where breeding was earlier passed through Mestersvig in early August. They fed on coastal tundra and the sea shore, probably mainly on small Diptera, and showed a strong tendency to flock with Ringed Plovers and other waders. Juveniles often attempted to flock with unfledged broods but were chased away by the parents. The adults, which probably left before their offspring, did not often join the coastal flocks.

The proportions of each 6 h period spent feeding by chicks at Mestersvig and Lindisfarne are shown in Figures 9 and 10. At Mestersvig, the feeding of chicks in the first half of the pre-fledging period tended to show a marked diurnal pattern with more feeding by 'day' than by 'night'. This pattern broke down later in the pre-fledging period. Heavy rain depressed feeding, as measured for the 7-day-old young. At Lindisfarne, data on the six hour periods 2400-0600 are very limited because of the difficulty in locating birds during the dark night and

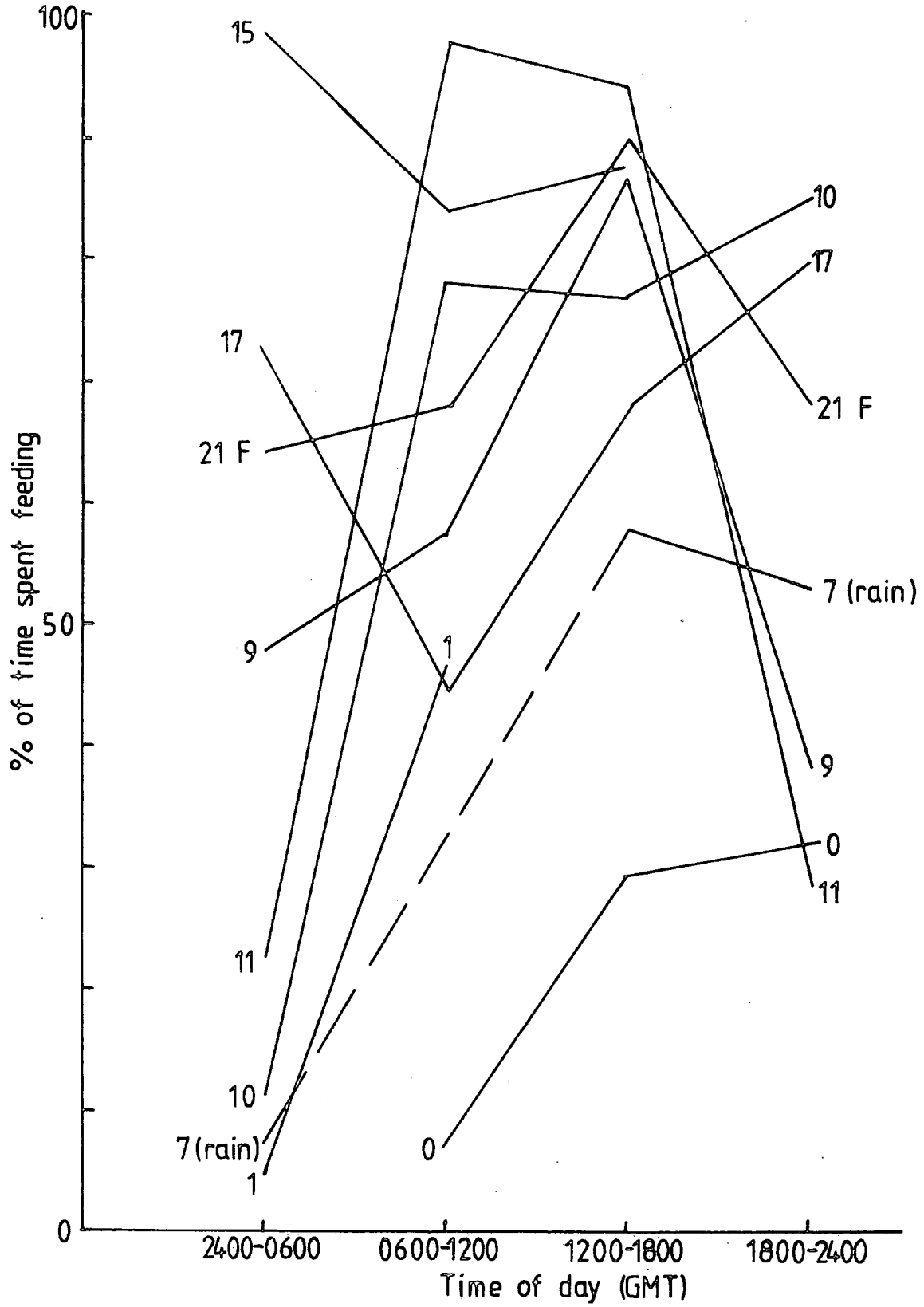


Figure 9. Proportion of each 6 hour period spent feeding by chicks at Mestersvig in relation to age.

Age in days indicated against each line.

F indicates fledging young.

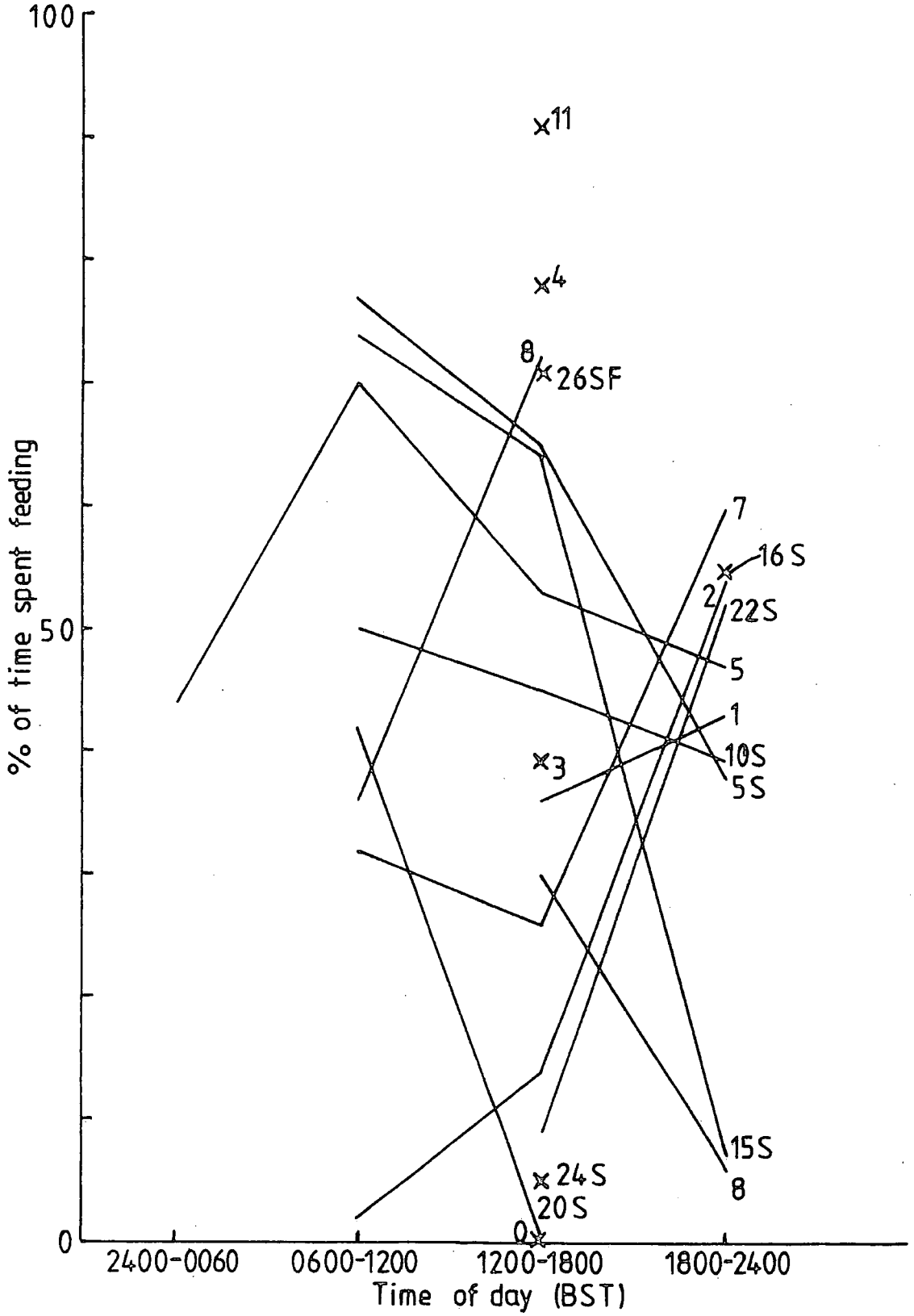


Figure 10. Proportion of each 6 hour period spent feeding by chicks at Lindisfarne in relation to age.

Age in days indicated against each line; F indicates fledged young; S indicates a brood at Snook End in 1976.

in early mornings. Although a diurnal pattern was apparent on some days, this was less marked than at Mestersvig.

Feeding time in each 6 h period increased significantly with air temperature at Mestersvig (Fig. 11, from which it can be seen that this applied at all ages) but not at Lindisfarne (Fig. 12) where the temperatures were generally higher. Feeding appeared to be depressed by rain at both sites, and high winds at Lindisfarne (these did not occur in the study period at Mestersvig).

The 24 h watches at Mestersvig allow estimation of the total time allocation of chicks throughout the pre-fledging period (Fig. 13), the proportion of the day spent feeding increasing from about 25% on the first day after hatching to 70% by the end of the period. At first, almost all the non-feeding time was spent being brooded, except for the brief periods of movement while not feeding and crouching during approach of potential predators. The brooding component decreased slowly for the first 10 days (less so during rain on the seventh day) and then markedly by 15 days of age to almost zero. Consequently, the time spent on, e.g. preening, non-brooded resting and roosting increased rapidly after about 11 days. A very small element of brooding remained until shortly before fledging.

Because of the lack of data in the 2400 to 0600 period at Lindisfarne, a similar diagram covering the whole day cannot be constructed. Instead, Figure 14b, based on the period 1200-1800 h, allows comparison with Figure 14a, based on the same time of day at Mestersvig. Figure 14a gives a fairly similar picture to Figure 13, allowing for the concentration of feeding during this, the warmest period of day at Mestersvig. The pattern at Lindisfarne showed some similarities, notably the increase in feeding during the first part of the pre-fledging period and the marked decrease in brooding from about 10-11 days onwards. Differences between the two areas were the greater variability at Lindisfarne (which appeared to result from the lesser diurnal rhythm than at Mestersvig) and the decrease in feeding at Lindisfarne around the time of fledging (which seemed to result from a tendency to fulfil feeding requirements early in the day where possible and rest in the afternoon).

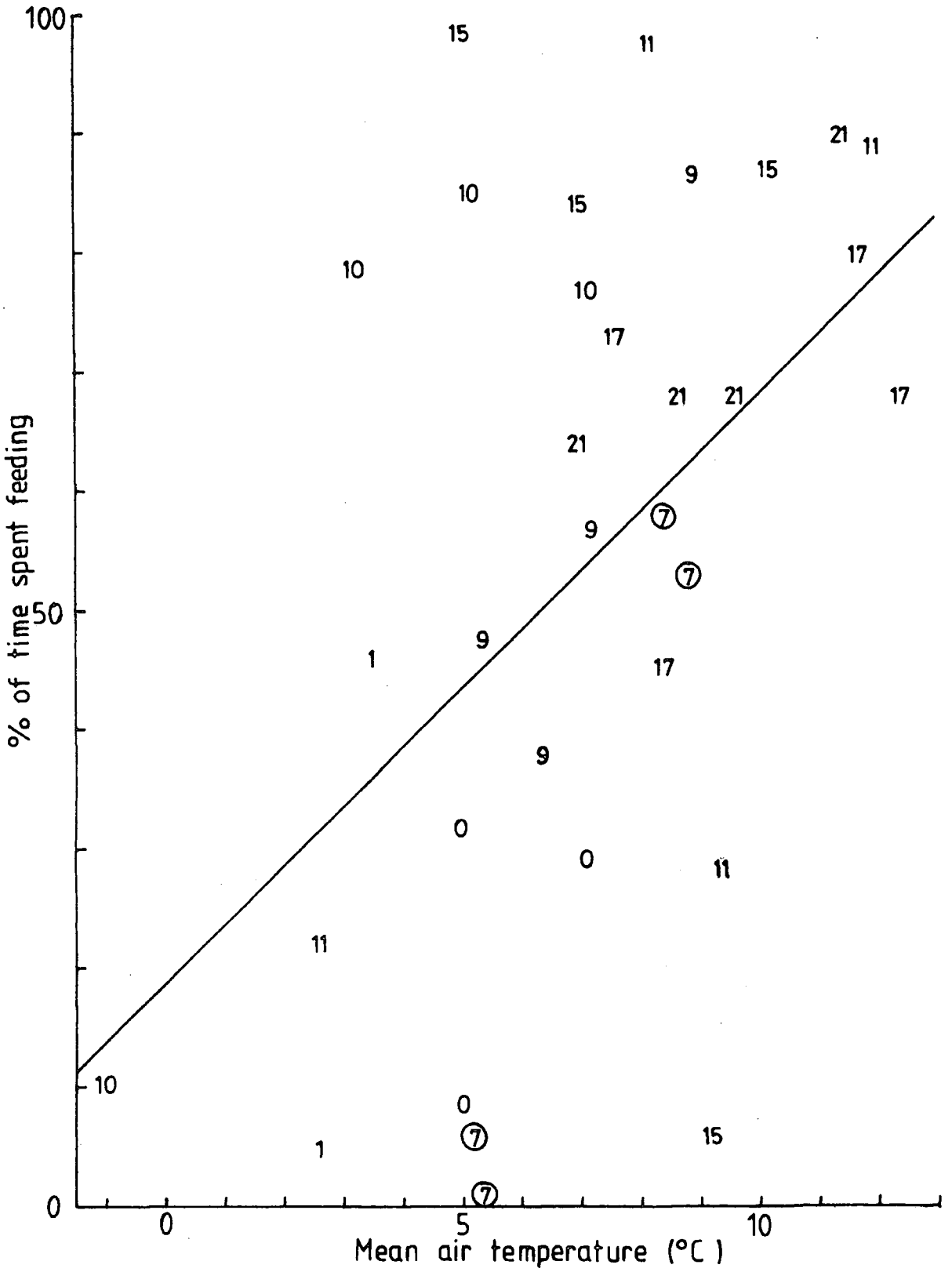


Figure 11. Proportion of each 6 hour period spent feeding in relation to mean air temperature during the period, at Mestersvig. Numbers indicate age in days. Circled figures indicate rainy day .

Regression line is $y = 5.0x + 18.8$ ($r = 0.49$, $P < 0.01$)

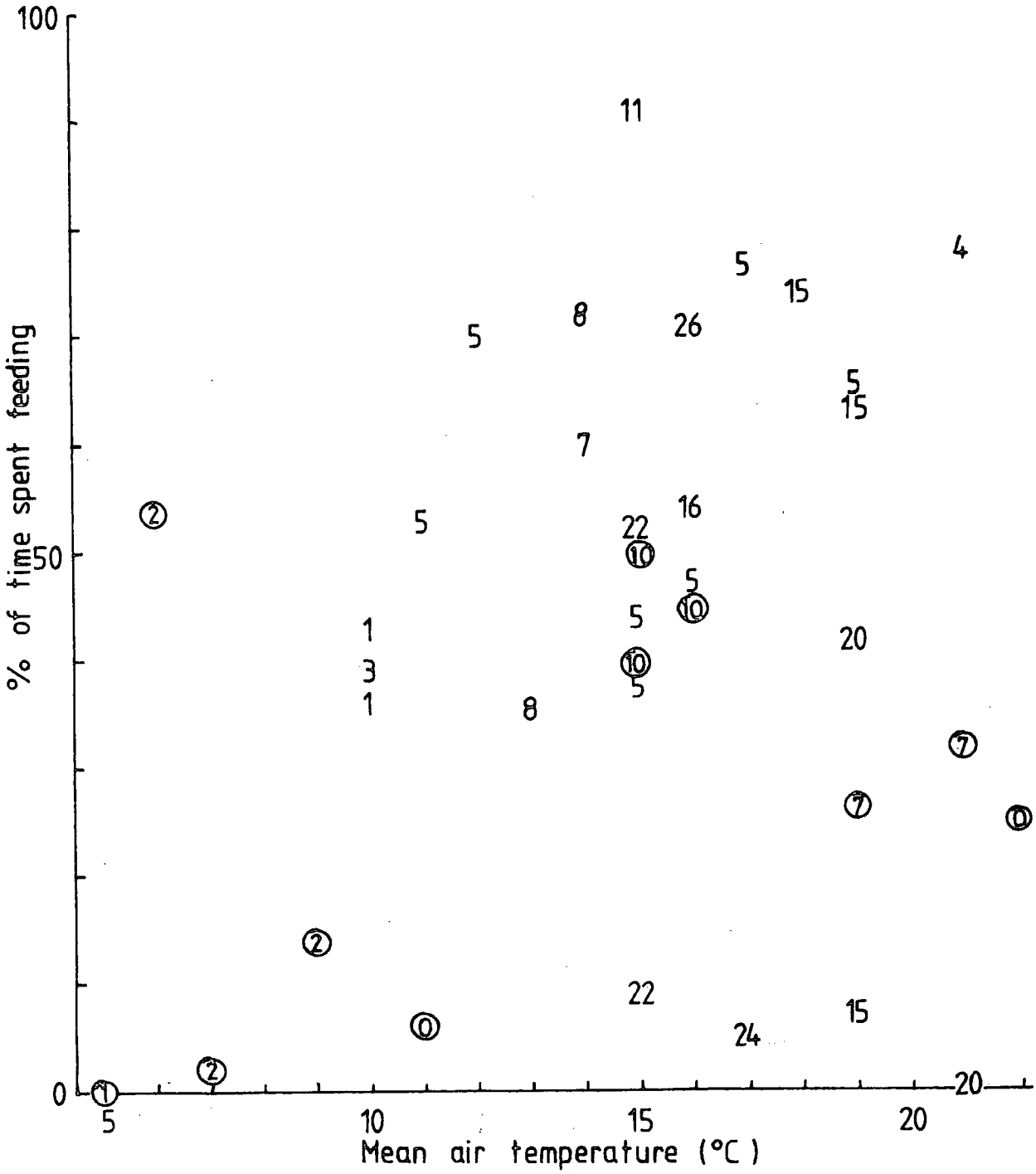


Figure 12. Proportion of each 6 hour period spent feeding in relation to mean air temperature during the period, at Lindisfarne.

Numbers indicate age in days. Circled figures indicate adverse weather.

r = 0.20, not significant.

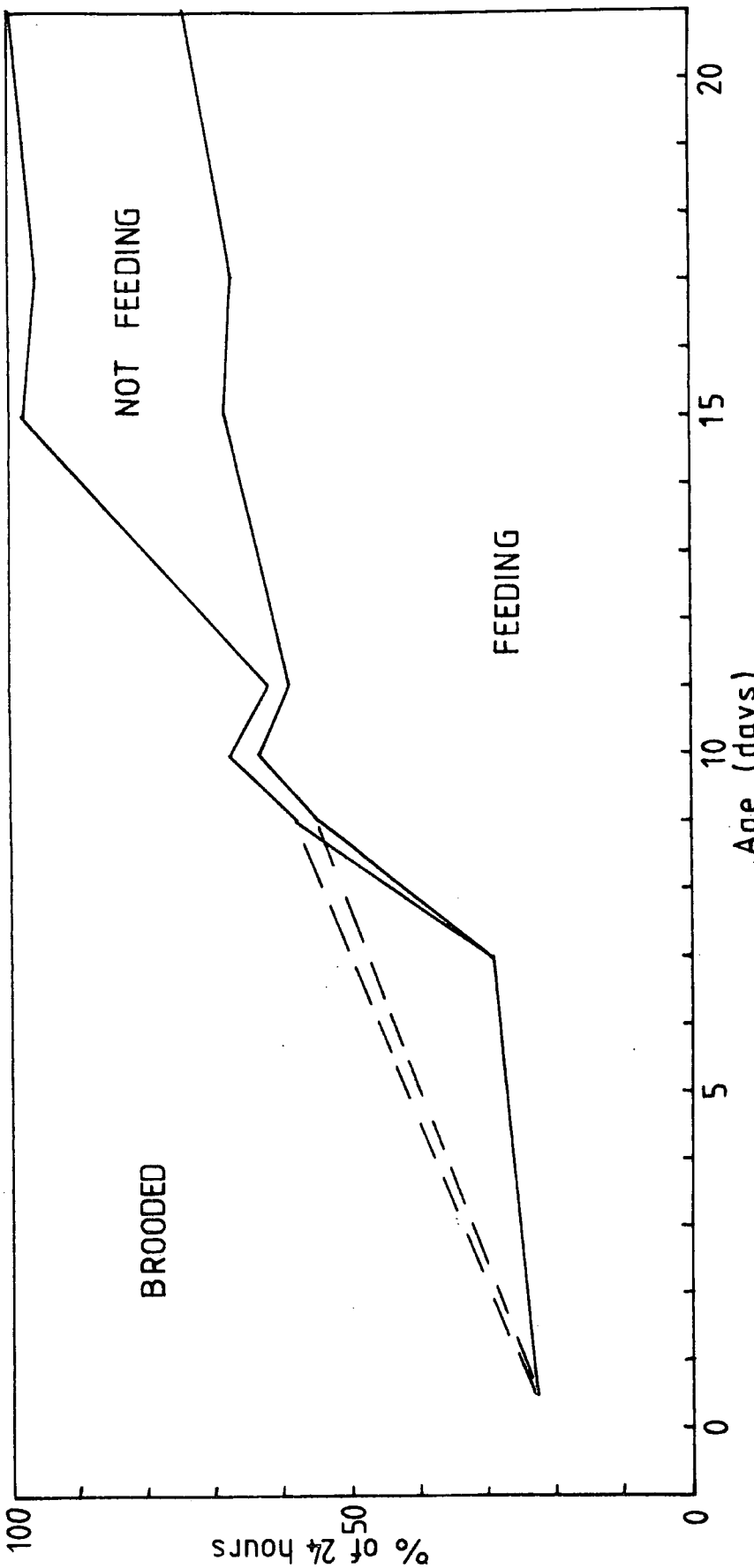


Figure 13. Time allocation per 24 hour period of chicks at Mestersvig. Note that rain fell throughout much of day 7.

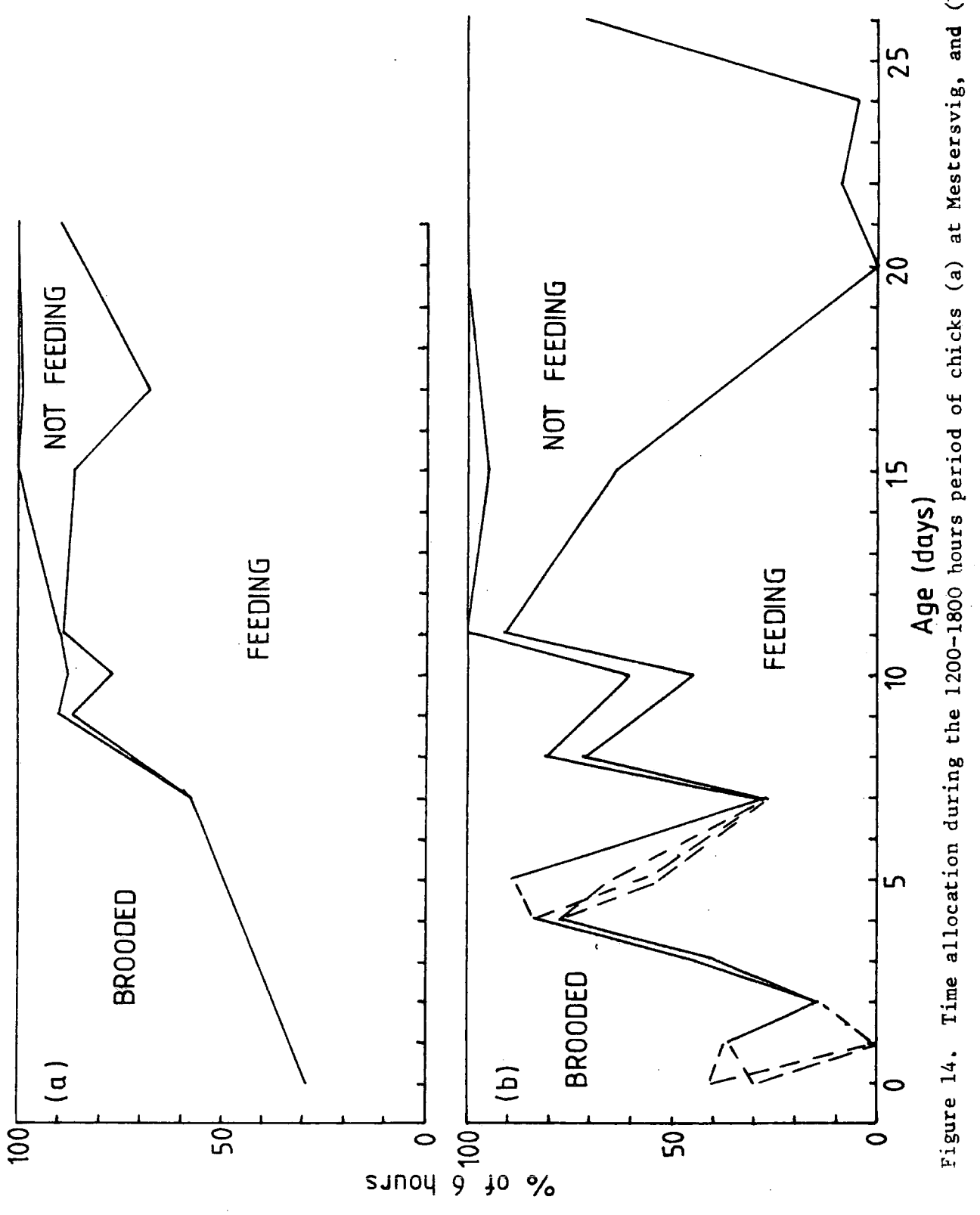


Figure 14. Time allocation during the 1200-1800 hours period of chicks (a) at Mestersvig, and (b) at Lindisfarne

The mean duration of non-brooded periods remained low at Mestersvig in the first week (Fig. 15) and at 'night' in the second week but increased markedly in the afternoon in the latter period. Chicks were brooded very little in the third week, and then only at 'night'. During the period of transition from much to little brooding (but not earlier or later), the time interval between broodings was more variable, possibly to some extent dependent on temperature. The pattern at Lindisfarne was fairly similar, although there were fewer data around the transition period (Fig. 16).

Prey composition

The outcome of pecks made by Ringed Plover chicks at Holy Island Snook are detailed in relation to age of chick in Table 3. Data on some fledged young of known age, identifiable by colour rings and feeding in the same area, are also included. Some of the variation displayed in the Table is undoubtedly due to variations in viewing conditions such that prey were less identifiable on some days. However, the high proportion of pecks with unknown outcome in very young chicks, particularly on the day of hatching and that following, suggests that a high proportion of pecks at this age were indeed unsuccessful, or that only very small prey were taken. Sandhoppers *Talitrus saltator* and small flies, mainly *Coelopa*, were the main prey identified from the fifth day after hatching onwards and these probably formed most of the unidentified prey taken even before this time. However, intertidal invertebrates were also taken, thin worms being noticed from 2 days after hatching, *Arenicola* from 5 days and *Hydrobia* occasionally. Although all *Arenicola* and many thin worms would have been identifiable, many smaller items probably were not. Feeding locations and methods suggested that other prey included small amphipods. The sizes of *Arenicola* taken are given in Table 4.

Comparison with prey taken by parent birds in the same area is difficult, since, as suitable viewing conditions and opportunities were limited, work was concentrated on the young and fewer prey of adults were identified (Appendix 1). However, there was clearly great overlap in range of prey types taken, although adults appeared to take a wider range and possibly a slightly higher proportion of intertidal prey.

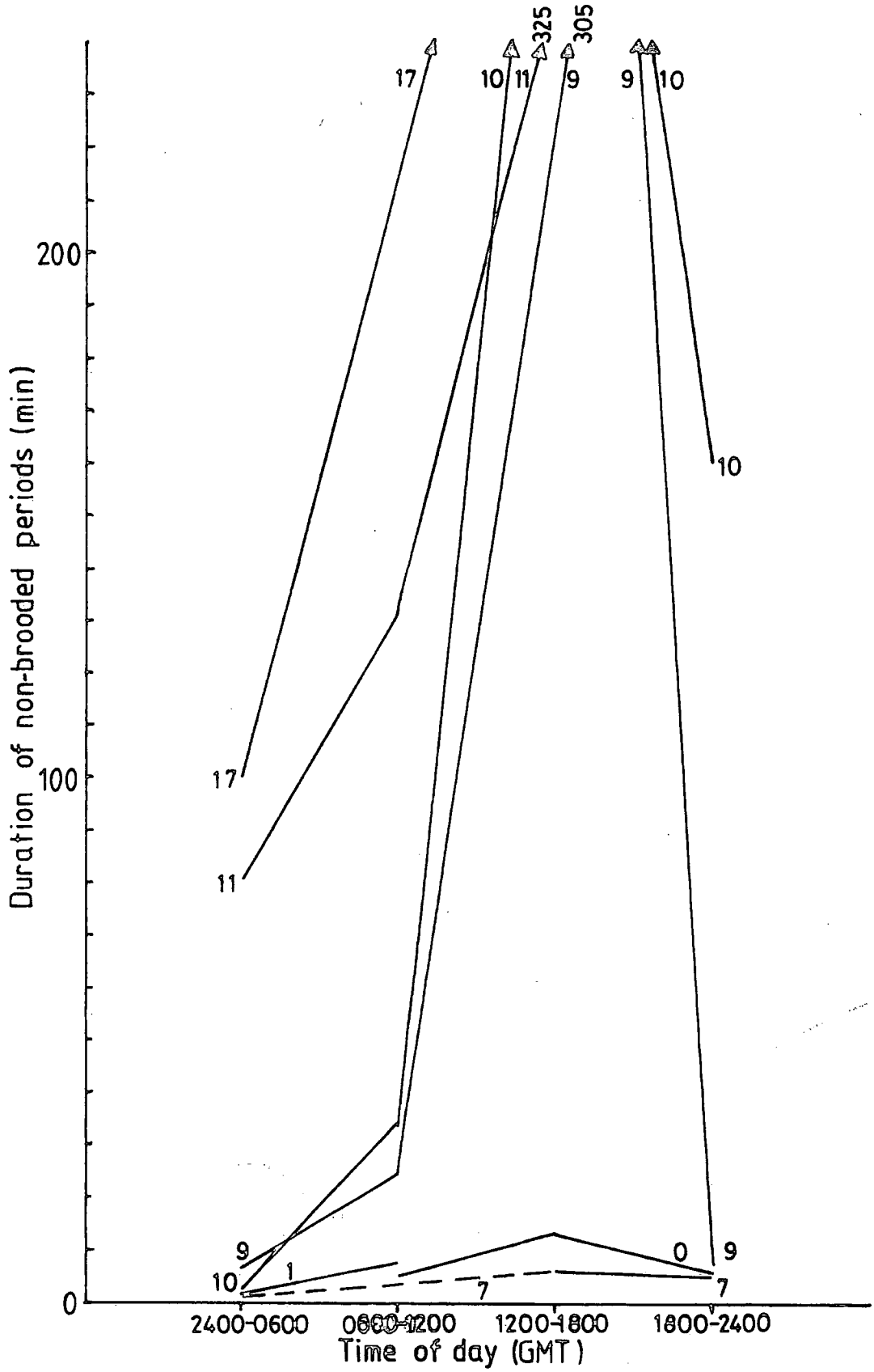


Figure 15. Mean durations of non-brooded periods of chicks at Mestersvig in relation to time of day. Figures indicate age of chicks. No brooding occurred after 0600 on day 17 or throughout days 15 and 21.

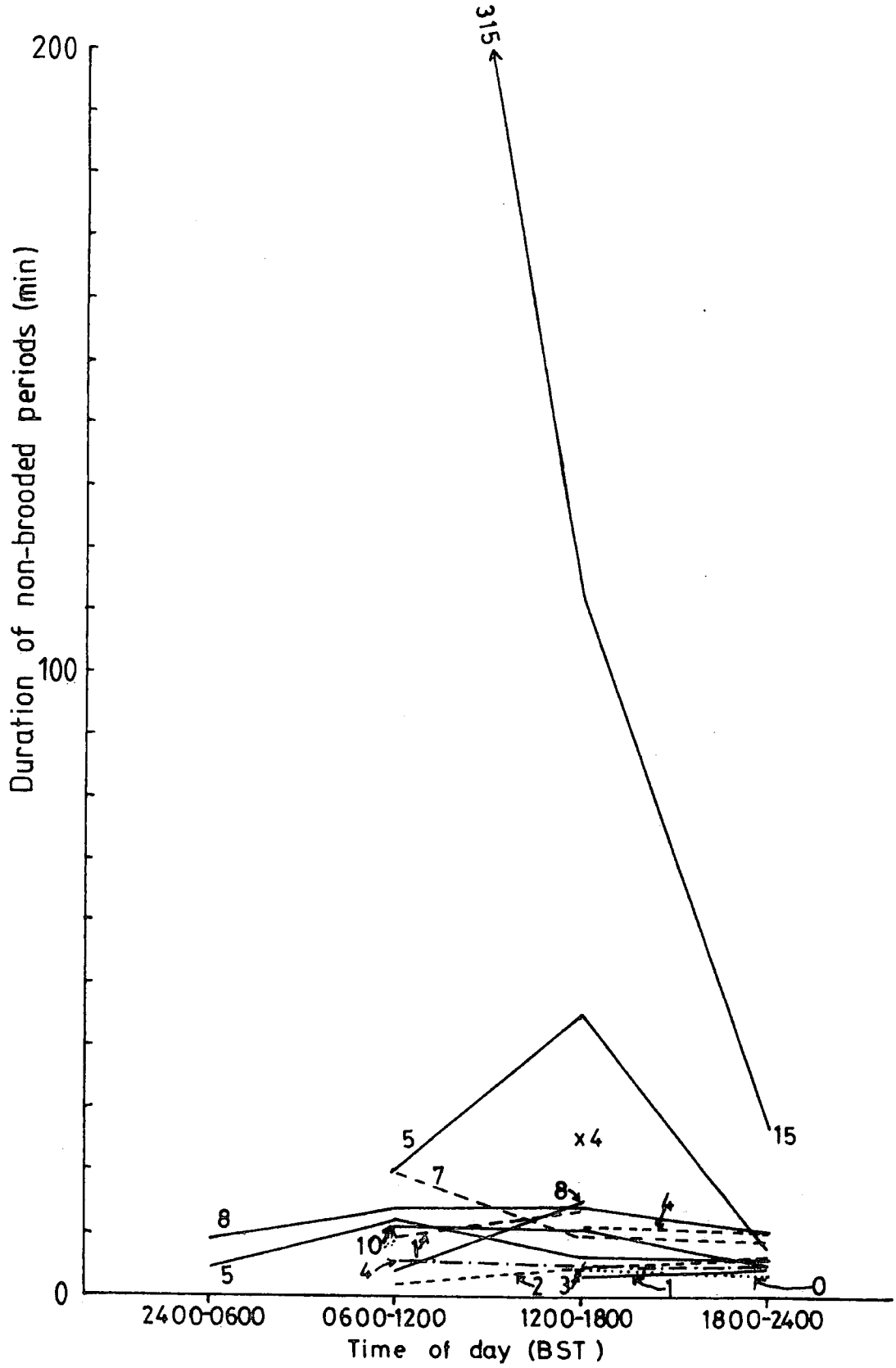


Figure 16. Mean durations of non-brooded periods of chicks at Lindisfarne in relation to time of day. Figures indicate age of chicks.

No brooding occurred on days 20, 22, 24 or 26 (the bird having fledged by day 26 if not before).

TABLE 3. SUMMARY OF PREY OF CHICKS AND NEWLY-FLEDGED YOUNG IDENTIFIED DURING FIELD OBSERVATIONS AT THE NORTH SHORE OF HOLY ISLAND SNOOK

Age of chicks (days)	0	1	2	3	4	5	6	7	9	10	15	16	20	22	24	26	28	31	40
Total pecks	57	794	206	266	9	928	70	405	68	372	962	23	261	211	72	105	33	20	35
Thin red worms	0	0	2	0	0	6	16	0	4	8	9	0	4	6	3	19	3	0	0
Arenicola	0	0	0	0	0	1	0	0	0	5	5	0	0	2	0	12	0	0	0
Sandhoppers	-	-	-	-	-	59	-	-	-	57	16	16	73	59	-	-	-	5	-
Small flies	-	-	-	-	-	23	-	-	-	24	167	4	-	71	-	-	-	-	-
Blowfly	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Hydrobia	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	2	-	-	-
Unidentified small prey	-	-	22	11	-	266	7	14	5	91	339	3	152	59	9	58	7	15	35
Pecks of unknown outcome	57	794	182	255	9	571	47	391	59	187	421	-	32	14	60	14	23	-	-
Unsuccessful pecks	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-

TABLE 4. NUMBERS OF *ARENICOLA* OF VARIOUS SIZES TAKEN BY RINGED PLOVER CHICKS AT HOLY ISLAND SNOOK

	Age (days)				
	5	10	15	22	26
Worm length (in relation to height of bill off the ground)[1]					
Fragment of tail only					2
< ¼ bill-height			3		
¼ " "					1
½ " "	1	2			3
¾ " "					
1 " "		2	2[2]		3
1¼ " "					1
1½ " "					1

[1]The height off the ground of the bill of a feeding Ringed Plover increases from about 5 cm to about 8 cm during the pre-fledging period.

[2]One bill-height worm taken at 15 days was not swallowed. Five worms were seen to be taken from the substratum tail-first and one head first.

Fewer data are available from sites at Lindisfarne outside the main study area at the Snook. These are summarized in Table 5. Birds were rarely observed closely enough to allow identification of prey. Items taken from the thick algal beds between clumps of *Spartina* at Tealhole appeared to include large insect larvae and pupae. Many of the items taken at Ross Back Sands and Old Law were thought to be sandhoppers and small flies; this seems likely from examination of prey available on the beach feeding areas. One small chick was found dead on the shore above the mud-flats at Elwick on 30 June 1973. Its gizzard contained fragments of at least 8 *Hydrobia*, 74 mandibles of *Nereis*, several fragments of vegetable matter and several grains of sand and small stones. *Hydrobia* and *Nereis* are both abundant in this area. Droppings of chicks from Snook examined contained numerous fragments of adult Diptera but no other identifiable remains. The problems of use of gut contents in the identification of prey are discussed in Paper 1. Most of the fledged young included in Table 5 were feeding on the flats either on Holy Island Sands or off Guile Point. The thin red worms typical of prey in these areas (Paper 1) were well represented.

The outcome of pecks made by chicks and adults at Mestersvig are detailed in Table 6. Again great variation is apparent in the Table due to varying observation conditions on different days. Birds were generally viewed from a greater distance than at Lindisfarne and fewer prey tended to be identified. However, on some days it was clear that most prey were very small adult Diptera (mainly Nematocera - midges, gnats, mosquitos, etc.) which were taken off the sand, soil or vegetation surface or occasionally in flight. Examination of feeding sites also suggested that these very abundant items were the main prey at other times also. Other fairly common prey identified were spiders Aranea and large items, probably large insect larvae including Lepidoptera.

Prey of adults at this time appeared to be fairly similar. Earlier in the season, fewer adult insects were probably taken (fewer had emerged) and possibly more spiders. Examination of feeding sites indicated that some of the small items taken in late June and July were dipteran larvae (again mainly Nematocera). Examination of gizzard contents of seven adult Ringed Plovers collected in the same area

TABLE 5. SUMMARY OF PREY OF CHICKS AND FLEDGED YOUNG OF KNOWN AGE IDENTIFIED DURING FIELD OBSERVATIONS AT LINDISFARNE AWAY FROM THE NORTH SHORE

	Teal Hole	Ross Back Sands and Old Law				Flats at Holy Island Sands and near Guile Point								
Age (days)	6	8	15	17	20	28	30	31	33	40	50	63	68	72
Total pecks	66	70	54	78	59	74	70	55	36	120	121	49	30	12
Thin red worms	-	-	-	-	5	-	1	-	9	3	5	10	7	1
Pecks at weed	7	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified small prey	1	33	16	26	13	23	7	32	11	115	5	33	13	7
Pecks of unknown outcome	58	37	38	52	41	51	62	23	16	2	111	6	10	4

TABLE 6. SUMMARY OF PREY OF CHICKS AND ADULTS IDENTIFIED DURING FIELD OBSERVATIONS AT MESTERSVIG

											Adults	
Age (days)	0	2	3	7	9	11	12	16	17	21	Jul	Aug
Total pecks	107	173	361	1447	1736	447	522	235	1935	3858	2010	891
Spiders	-	-	-	2	1	1	7	3	2	-	26	4
Large caterpillars	-	-	-	2	-	22	6	5	12	-	2	-
Small flies	-	-	-	-	-	25	-	-	646	2	158	335
Small unidentified prey	22	-	16	148	3	58	117	53	83	1923	128	285
Pecks of unknown outcome	85	173	345	1295	1732	341	392	174	1192	1933	1696	267

between 28 July and 21 August 1972 by R.W. Summers and G.H. Green supported this general assessment of diet. The only identifiable remains in a number of droppings of chicks examined were numerous fragments of small adult Diptera.

Feeding rates

At Mestersvig, the total pecking rate increased significantly with increasing age of chick and air temperature and decreasing rainfall (Table 7, Appendix 4). These relationships were paralleled by the variations in rates of taking identified insects, observed prey and pecks of unknown outcome (Table 7). These parallels resulted from the predominance in the diet of small flies throughout the period.

At Lindisfarne, both on the North Shore and elsewhere, total pecking rate did not vary linearly with chick age (Table 8, 9, Appendix 4) but this numerical measure appears to hide considerable variation due to the more varied diet in terms of both species and size. Rates of taking any prey (i.e. all pecks seen to be successful), *Arenicola* and thin worms all increased with increasing chick age and decreasing wind force, whereas rates of pecking with unknown outcome (in the main small prey or failed pecks) varied in the opposite direction (Tables 8, 9, Appendix 4). Rain also appeared to depress feeding rate, but as birds also tended to stop feeding during rain, the sample was too small to give significant results with individual prey types. Air temperature seemed to have little effect on feeding rate, though this possibly increased with temperature at low temperatures but decreased at higher ones (Appendix 4, Paper 2).

Diurnal temperature variation had a strong influence on pecking rate at Mestersvig, but at Lindisfarne, the fluctuations in temperatures occur around much higher levels and did not appear to influence pecking rate (Appendix 4).

Because of the overwhelming predominance of one type of prey (the very small flies) in the diet at Mestersvig, and the observations of feeding throughout 24 h periods, it is possible to make an estimation of the minimum energy intake of chicks at this site (Table 10). The mean dry weight of these flies was determined as 0.16 mg and the

TABLE 7. RELATIONSHIPS OF FEEDING RATES OF RINGED PLOVER CHICKS WITH AGE AND ENVIRONMENTAL CONDITIONS AT MESTERSVIG

For significant relationships, the correlation coeffiecient is given and the level of significance ($P < 0.05, 0.01, 0.001$) indicated after it by 1 to 3 asterisks. For those relationships which remained significant in stepwise multiple regression analysis, significance levels in that analysis are indicated before the coefficient.

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking insects
Age	*** 0.49***	*** 0.41***	* 0.13*	*** 0.37***	0.14***
Air temperature	0.36***	** 0.19***	*** 0.21***	*** 0.12*	0.17***
Wind force	-	-	**-0.09*	--	-
Rain	*-0.08*	-0.09*	-	-	-
Cloud cover	-	-0.22***	* 0.20***	-0.20***	-0.09*

TABLE 8. RELATIONSHIPS OF FEEDING RATES OF RINGED PLOVER CHICKS WITH AGE AND ENVIRONMENTAL CONDITIONS ON THE NORTH SHORE OF HOLY ISLAND SNOOK

Arrangement as for Table 7.

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking thin worms	Taking *Arenicola*	Making aborted pecks
Age	-	*** 0.46***	*-0.16*	*** 0.42***	*** 0.22***	0.36*	-
Air temperature	-	* 0.16*	-	* 0.16*	-	-	-
Windforce	-	-0.39***	*** 0.24***	-0.35***	-0.30***	**-0.31***	-
Rain	-0.15*	-	-	-	-	-	0.11*
Cloud cover	-	-0.16**	-	-0.16**	-	** 0.14*	-

TABLE 9. RELATIONSHIPS OF FEEDING RATES OF RINGED PLOVER CHICKS WITH AGE AND ENVIRONMENTAL CONDITIONS AT LINDISFARNE AWAY FROM THE NORTH SHORE

Arrangement as for Table 7.

Rates of:	Total pecks	Taking observed prey	Pecks of unknown outcome	Taking small prey	Taking thin worms	Taking *Arenicola*	Making aborted pecks
Age	-	0.37***	-	0.37***	0.21**	0.18*	-
Air temperature	-	-0.47*	0.49*	-	-	-	-
Windforce	-	-0.34***	0.41***	-0.36***	-0.19**	-0.20**	-
Rain	-0.12*	-	-0.12*	-	-	-	0.10*
Cloud cover	-	-	-	-0.17*	-	0.17*	-

TABLE 10. ESTIMATED ENERGY INTAKE PER 24 HOURS OF CHICKS AT MESTERSVIG

See text for discussion of limitations of these estimates.

Age (days)	Mean no. of pecks/min	% of 24h spent feeding	Mean no. pecks taken per 24h	Energy ingested/24h (kcal)	Mean weight of chick (g)	Basal Metabolic Rate (kcal) (from Keskpaik *et al.* 1970)	Intake as multiplier of BMR
0	8.0	23	2650	2.1	8	1.4	1.5
7	17.1	29	7140	5.7	19	4.8	1.2
9	19.7	55	15600	12.5	24	6.0	2.1
11	22.3	59	18950	15.1	29	6.6	2.3
16	28.8	68	28200	22.6	41	9.3	2.4
17	30.1	67	29040	23.2	44	10.0	2.3
21	35.3	74	37620	30.1	54	12.3	2.5

calorific value as 5 kcal/g, giving a value for an individual of 0.8 cal. All pecks were assumed to result in a prey item being taken and all prey items were assumed to be small flies. As other items were seen to be taken (Table 6) and the calorific contents of spiders and crane-flies are, respectively, more than 30x and more than 100x that of small flies (Greenwood 1974a, present study), the effect of the latter assumption considerably outweighs the former so that the energy intake figure obtained is an underestimate. Using values of Basal Metabolic Rate for chicks of various ages obtained experimentally by Keskpaik *et al.* (1970), Table 10 estimates the minimal total energy intakes as multipliers of BMR. This gives a value of 1.2 - 1.5 in the first week after hatching, rising to 2.1 on day 9 and stabilizing at 2.3 - 2.5 from day 11. While bearing in mind that these figures are probably underestimates, it is noteworthy that the values reach a relatively high level and stabilize around the time that the young become largely thermally independent.

Foraging behaviour

Aspects of the foraging behaviour of chicks at Lindisfarne are summarized in Table 11 in relations to age and weather conditions. Behavioural categories are described more fully in Paper 2.

Both waiting and giving-up times increased with age of chick, as did the frequency of 'successful' pauses ('up' followed by 'peck'). The frequency of 'unsuccessful' pauses ('up' followed by 'run' to another 'up') fell with increasing age (Table 11 & Appendix 4), as did the frequency of 'downs'. Handling time did not vary with age, although size of prey taken did tend to increase with age (see above). Number of paces (both to move position and to take prey) showed no significant trends with age or weather conditions, possibly due in part to small sample size. However, there was an increase in pace-length from about 6 cm shortly after hatching to about 10 cm when fully grown (measured from tracks of young of known age).

Increasing windforce was associated with decreasing waiting time in the 'up' position but increasing rate of 'unsuccessful pauses'. Despite the small number of observations during rain, the rate of 'successful' pauses decreased with increasing rainfall, and the rate of 'abortive pecks' increased. With increasing cloud cover both

TABLE 11. FORAGING BEHAVIOUR OF RINGED PLOVER CHICKS AT LINDISFARNE IN RELATION TO AGE AND ENVIRONMENTAL CONDITIONS

Arrangement as for Table 7.

	Age of chick	Air temperature	Wind force	Rain	Cloud cover
Giving-up time	0.23***	-	-	-	-0.21**
Waiting time	** 0.19**	-	-0.20**	-	-0.24***
Rate of "unsuccessful waits" ('up' followed by 'run' to another 'up')	***-0.57***	-	0.22***	-	* 0.30***
Rate of "successful waits" ('up' followed by peck with or without intervening run)	0.16*	-	-	-0.13*	-
Rate of 'downs'	-0.26***	-	-	-	0.12*
Handling times	-	-	-	-	-
Distance run to new 'up' position	-	-	-	-	-
Distance run to take prey	-	-	-	-	-

waiting and giving-up times decreased and rates of unsuccessful pauses and downs increased. There were no significant relationships with temperature but this was mainly above 12°C.

For the adults, with increasing temperature, increased waiting and handling times and a decreased rate of unsuccessful pauses occurred. Windforce was inversely related to rate of downs and distance run to take prey. With increasing cloud cover, the rate of successful pauses increased but handling time decreased. Foraging behaviour of fully grown birds was considered more fully in Paper 2.

The occurrence of foot-vibration as a foraging technique in the breeding areas at Lindisfarne is summarized in Table 12. Although this was recorded in a 10-day old chick and in another around fledging time, these were the only occurrences, whereas foot-vibration was frequent in parent birds in the same areas over the same period. These differences were significant. Foot-vibration was not recorded in adults or young at Mestersvig.

The feeding behaviours of fledged young and older birds at Lindisfarne from late summer onwards are compared in Table 13. In August and September, the only significant difference detected was a higher incidence of 'downs' in young birds (as tended to occur also in pulli - see above). In October-November the rate of pecking (and rate of 'ups') was significantly higher in adults than young. In December-February, although pecking rates were similar, there was some indication that prey taken by juveniles tended to be smaller. (By this time, numbers of identifiable young were small as many birds of the British population assume plumage very similar to adults in autumn.) No significant differences were apparent in March-May.

Pre-fledging mortality and survival

The survival rate to fledging of cryptic nidifugous young is notoriously difficult to measure and few estimates have been made for waders. Only data from closely watched and individually identifiable broods are used here and only from those families observed from before hatching until their fate was definitely known (Table 14).

TABLE 12. NUMBERS OF CASES AT LINDISFARNE IN WHICH FOOT-VIBRATION WAS USED AND NOT USED BY RINGED PLOVERS

		Chicks; age given in days													
		0	2	3	5	7	9	10	15	16	20	22	24	Fledged Young	Territorial adults
Snook	no vibration	10	20	4	35	14	3	18	19	1	-	9	0	3	123
	vibration	0	0	0	0	0	0	1	0	0	-	0	1	0	27
Other areas	no vibration										6			22	11
	vibration										0			0	8

Foot-vibration was significantly more frequent in adults than young ($\chi^2_1 = 19.8$, $P < 0.001$).

(Foot vibration was observed on no occasions at Mestersvig.)

TABLE 13. COMPARISON OF FORAGING BETWEEN RINGED PLOVERS IN THEIR FIRST YEAR AND OLDER BIRDS

Comparisons between age groups were made of the following rates: making pecks, of taking small prey, of taking thin worms, of taking *Arenicola*, of assuming 'up' positions, of assuming 'down' position.

The comparisons were made for the following seasons: August, September, October and November, December to February, March to May.

Only the following comparisons showed statistically significant differences:

Rate (min^{-1})	Juvenile[1]	Student's t (P)	Post-juvenile[1]
August			
'Downs'	1.30 ± 0.19 (65)	5.17 (< 0.001)	0.26 ± 0.08 (87)
September			
'Downs'	0.67 ± 0.18 (40)	2.10 (0.039)	0.23 ± 0.11 (38)
October/November			
Total pecks	13.88 ± 0.65 (57)	2.30 (0.023)	16.38 ± 0.87 (62)
'Ups'	16.93 ± 1.16 (57)	2.16 (0.033)	20.46 ± 1.16 (62)
December to February			
Small prey taken	5.93 ± 1.24 (21)	2.47 (0.014)	3.11 ± 0.36 (188)
(Total pecks	13.84 ± 1.92 (21)	(n.s.)	14.38 ± 0.65 (188))

[1]Given as mean ± standard error (sample size)

At Mestersvig, three broods, each initially of 4 young, were followed. These fledged 0, 3 and 3 young respectively. At least one chick of the unsuccessful brood was seen to be injured and limping for some time and it is suspected that this brood may have suffered from human interference. There is also circumstantial evidence that the loss on one chick from one of the other broods was due at least partially to human interference. The actual agency of death is not known. Potential predators in the area included Arctic Fox *Alopex lagopus*, Stoat *Mustela erminea*, Gyr Falcon *Falco rusticolus*, Long-tailed Skuas *Stercorarius langicaudus*, Glaucous Gull *Larus hyperboreus* and Raven *Corvus corax*, although none were seen to take chicks. The chicks' cryptic plumage when they crouched, combined with the adults' distraction displays towards ground predators and mobbing of aerial predators appeared to provide effective protection. All non-surviving chicks died within the first week after hatching. There is reason to believe that the predation rate of wader eggs and young were inflated over that typical of this area of NE Greenland because of the presence of high densities of predators around Mestersvig station where they were sustained, particularly overwinter, by food gathered by scavenging (Ferns 1978b). Other studies, with small sample sizes, also suggest fairly high survival of Ringed Plover young in northerly parts of their range (see Boyd 1962).

At Lindisfarne, a larger sample of broods was studied. Average survival in different areas and years varied between 40% and 60%, overall 45% (Table 14). In 1976 (the only year when sample size throughout the season was adequate to test this), survival of late hatching young was significantly less than that of early hatching young (Table 15). Most rates are somewhat lower than the 59.9% of Laven (1940) and much lower than the maximum of 77% estimated by Prater (1974) by an indirect method, which he conceded was likely to include a systematic error leading to an overestimate of survival.

Cause of death is known for only 2 broods (8 young) in 1976 when exceptionally high tides flooded the whole of an area which was normally an island at high water. No cases of successful predation of young were observed despite many hours of watching. Several predation attempts by gulls, usually Black-headed *Larus ridibundus* were observed,

TABLE 14. PERCENTAGE OF YOUNG WHICH SURVIVE FROM HATCHING TO FLEDGING

	No. of broods watched	No. young hatching	No. of those fledging	Percentage
NE Greenland 1974	3	12	6	50%
Lindisfarne 1975				
Snook	8	20	8	40%
Ross Back Sands & Old Law	5	20	8	40%
All Lindisfarne	14	43	19	44%
Lindisfarne 1976				
Ross Back Sands & Old Law	13	42	25	60%
All Lindisfarne	18	57	26	46%
Lindisfarne 1975 & 1976	32	100	45	45%

TABLE 15. PERCENTAGE OF YOUNG FLEDGING IN RELATION TO HATCHING DATE, ROSS BACK SANDS & OLD LAW 1976

	No. fledging	No. dying	Total	% fledging
Hatching up to 16 July	20	7	27	74%
Hatching after 16 July	5	10	15	27%
Total	25	17	42	57%

$\chi^2_1 = 6.64$ $P < 0.01$

often while chicks were swimming across stretches of water but the parent birds always deterred the attack by flying at the predators. Presumably, attacks by several gulls at once might be more successful but this was not observed. Carrion Crows *Corvus corone* were also possible predators but no attacks were observed. Most losses of chicks appeared to take place at night (despite the short period of darkness at this season). Foxes *Vulpes vulpes*, Brown Rats *Rattus norvegicus* and Short-eared Owls *Asio flammeus* are amongst the possible predators known to be active in this area at night.

Because of the difficulties of observation, the actual dates of death were often difficult to ascertain but of those where reasonable estimates were made, 19 (53%) died within the first week after hatching, 15 (42%) in the second week and only 2 (5%) in the third.

Post-fledging survival

Estimation of post-fledging survival rates over the first year of life of young waders are difficult to obtain from ringing returns because ringing may take place at any time in the pre-fledging period, when much of the mortality occurs. Many calculations (e.g. Laven 1940, Rittinghaus 1956, Wilcox 1959, Lenington & Mace 1975) have been based on returns of ringed pulli. However, survival of these birds until one year old involves an unknown and variable component of the pre-fledging survival rate plus the post-fledging rate. This is illustrated in Table 16 where the apparent decline in survival from 1973 to 1978 is attributable largely to a switch towards ringing chicks at a younger age in later years.

This problem in estimating the survival from fledging to about one year old may be overcome by considering the survival of only those colour-ringed chicks known to have fledged (i.e. those fledging from broods which were the subject of detailed observations and others seen alive within a few days of fledging - Table 17). This Table treats all returns as if they had occurred at one year old, although strictly a small correction should be applied for the one bird (4%) sighted for the first time at two years old. Allowance for this would increase survival rate from 57% to 59% . This survival rate includes one bird settling elsewhere in the Northumbrian coast. With the help of local observers,

TABLE 16. MINIMUM SURVIVAL FROM RINGING TO FIRST RETURN TO LINDISFARNE OR OTHER TERRITORIAL AREA OF BIRDS RINGED AS CHICKS

Year of hatching & ringing	No. of chicks ringed	No. sighted in a subsequent year[1]	% apparent survival
1973	7	3	43
1974	15	5	33
1975	46	17	37
1976	58	13	22
1978	18	4	22
Total	143	42	29

[1]Most first sightings were at one year old and most at Lindisfarne (see Tables 18 & 22)

TABLE 17. SURVIVAL FROM FLEDGING TO ONE YEAR OLD OF CHICKS RINGED AT LINDISFARNE

Year of hatching & ringing	No. colour-ringed chicks known to fledge	No. of these sighted following year	% survival fledging to one year
1973	1	0	0
1974	3	2	67
1975	15	10[2]	67
1976	23	12[3]	52
Total	42	24	57

[2]includes one bird settling at Low Newton, Northumberland

[3]includes one bird first sighted in third year (few observations made in second year)

checks have been made over much of the coast of NE England and SE Scotland. Of all chicks marked at Lindisfarne during the main study (i.e. not only those known to fledge) 3 were found on territory (when one-year-old) elsewhere in Northumberland and one probably on territory in Fife (Table 18). Additionally, one chick marked in 1977 after my main study had been completed was found in the breeding season in 1979 in East Lothian, and a chick marked at Lindisfarne in 1976 was present in that area during the 1980 breeding season (Fig. 17).

Of 21 colour-ringed one-year-old birds seen prospecting for or holding territories, 12 (57%) were seen again the following year (only years for which there was detailed checking two years after ringing being considered) (Table 19). No such birds were seen in following breeding seasons except in the general vicinity of the sites where they were seen when one year old. Notably some young also visited territories in many parts of the study area after fledging and may have been investigating areas for future use as breeding areas (cf Brewer & Harrison 1975). Return rates of males and females were similar, as were return rates of birds seen only prospecting and those holding territory. Of a small sample of 4 older birds, all returned in the following season (Table 19), suggesting higher survival in later years. This is supported by a consideration of the return rates of birds marked as breeding adults of unknown age (Table 20). The increasing return rate from year to year is not unexpected in view of the results from birds ringed as chicks, and tends to support the view that ring wear and loss was not a problem in this study. (In fact only one case of partial loss of colour rings was noted during the main study.) Of 21 nesting males of unknown age, all returned the following year but only 15 (79%) of nesting females of unknown age. None of the non-returning birds were found elsewhere.

Recruitment to the breeding population and uptake of territory

Most birds attempted to gain a territory and breed when about one year old, 70% acquiring a territory and nesting then, the rest at two years old. Many of the latter had attempted to gain a territory the previous year (Tables 19, 21). Birds spread throughout the study area and to a lesser extent outside, although there is possibly a slight tendency towards return to the natal site (Table 22). Birds,

TABLE 18. AGES OF RINGED PLOVERS SEEN FOR THE FIRST TIME IN POTENTIAL NESTING AREAS

Year of hatching & ringing	Years later when first sighted		
	1	2	3
1973	1		
1974	5[1]		
1975	16[2]	1	
1976	12[3]		1[4]
Total[5]	34	1	1[4]

[1]includes 1 bird at Eden Estuary, Fife

[2]includes 2 birds at Low Newton, Northumberland

[3]includes 1 bird at Craster, Northumberland

[4]few sightings were made two years after ringing and the bird may have returned then

[5]includes 32 at Lindisfarne and 4 elsewhere (i.e. 11% elsewhere)

TABLE 19. SURVIVAL OF RINGED PLOVERS OF KNOWN AGE AFTER THE FIRST SUMMER OF LIFE

Year of hatching & ringing	No. seen at 1 year old	No. of these seen at 2 years old	% survival 1 to 2 years old	No. (%) surviving from 2 to 3 years old	No. (%) surviving from 3 to 4 years old
1973	1	1	100	1(100)	1(100)
1974	4	2	50	2(100)	
1975	16	9	56		
Total	21	12	57		
Males	9	6	67		
Females	8	4	50		
Sex not determined	4	2	50		

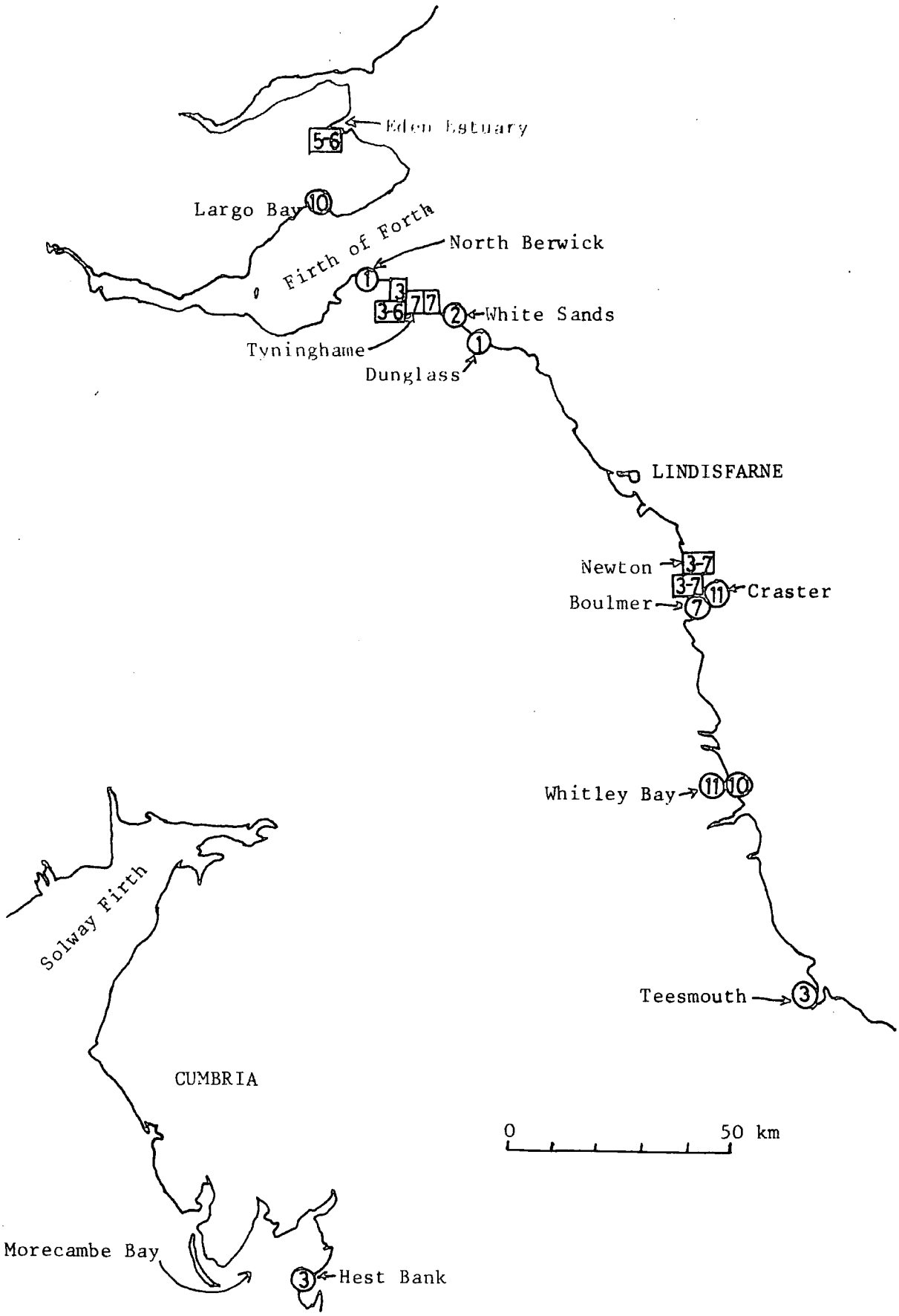


Figure 17. Sightings of Lindisfarne-marked Ringed Plovers elsewhere (see also Table 26).

Figures indicate month of sighting; those in square boxes indicate where the birds were thought to be establishing territory, or trying to.

TABLE 20. SURVIVAL OF NESTING ADULTS[1]

Year of ringing	No. recorded in year:			
	0	1	2	3
1974	2	2	2	2
1975	18	15	14	
1976	1	1		

Years after ringing (x)	0	1	2	All
No. recorded x years after ringing	21	17	2	40
No. recorded following year	18	16	2	36
Survival in relation to years after ringing	86%	94%	100%	90%

Total nesting bird-years of unknown age	40 - 36 (90%)
Total nesting bird-years of known age[2]	25 - 16 (64%)
All nesting bird-years	65 - 52 (80%)

Survival in relation to year of birds ringed as adults

74 - 75		75 - 76		76 - 77	
2	2	20	17	18	17
100%		85%		94%	

Survival in relation to sex of birds ringed as adults

Males	21/21	(100%)
Females	15/19	(79%)

[1]This Table refers to birds ringed as adults, except as indicated by 2.

[2]This line refers to birds ringed as chicks and later found as nesting adults.

TABLE 21. AGE OF FIRST RECORDED NESTING

Year of hatching & ringing	Age at first recorded nesting	
	1	2
1973	1	
1974	2	2[a]
1975	11	4[b]
Total	14 (70%)	6 (30%)
Males	6 (83%)	1 (17%)
Females	4 (80%)	1 (20%)
Birds of undetermined sex	1 (33%)	2 (67%)

[a] both seen at Lindisfarne 'prospecting' when one year old

[b] three seen at Lindisfarne 'prospecting' when one year old

TABLE 22. SITES OF TERRITORY ESTABLISHMENT IN RELATION TO NATAL AREA

	Number of birds settling at:									
Hatched:	Goswick	Snook	Guile Point	rest of Old Law	Ross Back Sands	Elwick	Chare Ends	Sandon Bay	Newton, Northumberland	Eden Estuary, Fife
Goswick			1							
Snook		3	4			1	1	1		1
Guile Point		1		1			1			
rest of Old Law	1		1	1					1	
Ross Back Sands		1	2	3	1					
Tealhole									1	
Sand Rig		1								

particularly one-year-olds, may move around to several sites within a season before establishing a territory or failing to do so (Table 23).

Once a territory had been established birds tended to return to that vicinity (and particularly in some parts of the Lindisfarne Reserve to the same territory) in following years (Tables 24, 25). Three sightings in later years of colour-ringed birds in the areas of marking give evidence for a tendency to site-fidelity in Greenland (Green 1978b), although systematic checks of nearby areas to look for changes of site could not be made.

Mate fidelity

There were several cases of change of mate between years but most of these involved cases in which either one bird was not individually identifiable or one of the pair was not seen in the later year. However, the high degree of site fidelity, in some sites at least, by both sexes suggests that mate fidelity may also tend to occur. There were only two cases in which both birds of a pair were marked and both returned the following year. In one instance, these remained as a pair. In another case a female was paired to an unringed male (not necessarily the same one) in three years and to two different marked males in the next two years. The mate of the fourth year nested in the same territory in the fifth year, with a new female. The old female frequently changed territory in the five years (RW/RM in Table 23). Laven (1940) found only two pairs mated for two seasons out of 54 marked adults studied for 4 years, but Kozlova (1961) reported that pairs stay together for several years, though she did not give details of the studies on which this conclusion was based.

Wintering

Greenland-breeding Ringed Plovers migrate through Britain in August - September and May and probably winter in W. Africa (Green 1978, Pienkowski in press).

Most Lindisfarne breeding birds leave their territories in late July or August and move on to the main intertidal flats. Many of the adults start primary moult while breeding and continue it at this time and many young birds undergo a partial moult to acquire plumage very

TABLE 23. EXAMPLES OF BIRDS APPARENTLY PROSPECTING PRIOR TO TAKING UP TERRITORY AND MOVES OF TERRITORY

RW/RM (♀)
Ringed as chick 15 July 1973 at Sand Rig
Held territory and nested first at Goswick, then on west part of N Shore 1974 and in feeding flock on Holy Island Sands in October 1974
1975:
late March and early April on territory at W end of Snook
24 April chased from E. part of N Shore by territorial birds and later seen in feeding flock near Sand Rig
20 May found nesting at Tealhole. Hatched and reared 3 young which fledged in late June
9 July scraping on shore at Snook Point. (On same day, unmarked pair were holding Tealhole territory.)
early September - late October seen in feeding flocks at Rig, N Shore, Holy Island Sands and Sandon Bay
1976:
Territory at Snook End

RB/WM (♂)
Ringed as chick 25 June 1974 on North Shore
Feeding on Holy Island Sands on numerous occasions from 2 September 1974 to 26 January 1975 (moulted from juvenile to adult plumage between 2 September and 16 October 1974).
1975:
20 January Sandon Bay
26 January displaying near Chare Ends
27 February North Shore
3 March onwards through May holding territory at Chare Ends

RW/WM (♀)
Ringed as chick 25 June on North Shore
1975:
20 January & 8 April Sandon Bay but not defending territory
23 June feeding on E. North Shore but not territorial and chased off
August to December feeding in flocks at Guile Point, Holy Island Sands, Sandon Bay

YW/WM (♂)
Ringed as chick 25 June 1974 on North Shore
1975:
6 May in flock on Beal Sands
22 June feeding briefly on E. N Shore but chased off from territory to territory westward along shore to Snook End, and from there
September & October in flock on N Shore and Holy Island Sands
1976:
on territory on W. North Shore all season

GB/BM (♀)
Ringed as chick 12 June 1975 on North Shore
1976:
16 June apparently prospecting at Guile Point
29 June apparently prospecting at Snook End
apparently no permanent territory in 1976
1977:
1977 onwards held territory near Guile Point

RO/MB (♂)
Ringed as chick 1 August 1975 Goswick
1976:
February to March feeding in flock on Holy Island Sands
29 April near Guile Point
30 April apparently prospecting at Tealhole
24 June nesting on Sandon Bay

GB/MO
Ringed as chick 7 August 1976 SW Old Law
Throughout summer 1977 seen on numerous occasions on Snook and Old Law
Throughout summer 1979 on territory on North Shore

TABLE 24. TERRITORY FIDELITY OF ADULTS OF UNKNOWN AGE

Initial site	No. of marked birds at initial site & seen following year	No. of these returning to initial site 1 year later[a]	No. returning to initial site 2 years later	Birds changing territory area
Goswick	2	2	2[b]	1[c]
Snook	6	6[f]	4	1[d]
Ross Back Sands	3	3[f]	1	1[e]
Old Law	5	5		

[a]All returning Snook birds returned to the same territory, as did 3 of Old Law birds (1 SE Old Law, 2 Guile Point) in both years, and 1 in one year (Guile Point). Other Old Law birds (E. Old Law) and birds from other areas returned to the same general area but not the same territory.

[b]Also returned 3 years later

[c]This bird had successive territories in year 2 at (i) Goswick, (ii) Snook & (iii) Rig and in year 3 at Goswick

[d]This bird moved in year 3 to Wideopens where it had visited in year 2

[e]This bird moved in year 3 to SE Old Law

[f]One bird from each of these groups not seen in subsequent year

TABLE 25. TERRITORY FIDELITY OF ADULTS OF KNOWN AGE

Initial Territory area	No. returning to this area in following year[a]	No. moving to other area
Snook	3[b]	0
Old Law	2	1[c]
Sandon Bay	0	1[d]
Newton	2	0

[a] all returns were to about the same territory

[b] data available for one pair of years for each bird except one in this group. This bird established territory again at Snook in year 2 but moved later in season to Tealhole before returning to Snook territory, where it held territory again in years 3 & 4

[c] one move from NE Old Law to Goswick

[d] one move to W Old Law

similar to that of adults. Many individuals leave the area between August and October, returning from February to April or even May but some birds stay in the area over the winter(Table 26). These differences do not appear to be age-related. Those birds which depart appear to disperse mainly along the coast of NE England and SE Scotland and to a lesser extent to the nearest parts of the W coast (Table 26, Fig. 17). The birds of the NE England/SE Scotland coast are probably among the more thoroughly watched in the country but there is other indirect evidence that Lindisfarne Ringed Plovers do not spread much further. This comes from sightings elsewhere in Britain of Ringed Plovers marked in East Germany by similar methods over the same years in approximately similar numbers (Dr A. Siefke, *in litt.*). Four sightings of these birds have been made in S. England, S. Ireland, and Channel Islands but none in those areas of birds marked in the present study.

DISCUSSION

Activity patterns, feeding and growth

One reason frequently given for the northern breeding distributions of some birds is that continuous daylight allows uninterrupted feeding and rapid growth of the young (e.g. Karplus 1952, Armstrong 1954, Welty 1962, Thomson 1964, Lack 1968, Dorst 1974). In the present study, however, growth rates of Ringed Plover chicks were remarkably similar at Lindisfarne, in Greenland and in other areas, and the diurnal pattern of feeding activity was more marked in the Arctic than in temperate breeding grounds, where some feeding took place in darkness (Paper 2). In the Arctic, such a diurnal pattern is typical both of other waders, e.g. Semipalmated Sandpiper *Calidris pusilla* (Safriel 1975), and non-waders e.g. Snow Buntings *Plectrophenax nivalis* and Wheatears *Oenanthe oenanthe* (Summers 1972, 1974, Asbirk & Franzmann 1978a,b). Further, Maher (1964) found little difference in growth rates in arctic and temperate finches, and Ricklefs (1968) summarized similar data for various species.

Several features support the argument that food supply was not limiting growth rate or chick survival (cf Ricklefs 1968, 1969): the constancy of growth rates (Figs. 6-8); the abundance of available prey (Papers 1 and 4, Appendix 5, Greenwood 1978); the 'unused' potential

TABLE 26. SUMMARY OF WINTER OBSERVATIONS AND OF SIGHTINGS AWAY FROM LINDISFARNE

Approximate dates of last and first sightings are given only when observations covered appropriate areas around these times. Settling (and breeding season sightings) away from Lindisfarne are underlined. Note that continuous coverage ended September 1976.

Individual	Year of hatching (or ringing)	Month of last sighting in autumn	Month of first sighting in spring	Observations away from Lindisfarne & Notes
RW/WM ♀	1973	end Oct 74, end Oct 75	late Feb 75, early Mar 76	
RO/CM ♂	(1974)	Sept 75, Aug 76	May 76, Mar77	
RY/GM ♂	(1974)	mid Oct 75	early Mar 76	Probably stayed 74-75 winter
WG/WM	1974			Eden Estuary, Fife May-June 1975
RY/WM ♀	1974			Probably stayed 74-75 winter
RB/WM ♂	1974			Stayed 74-75 winter
RW/WM ♀	1974			Stayed 74-75, 75-76, 76-77 winters
YW/WM ♂	1974	Oct 75	Mar 76	
W/YM	(1975)			Whitley Bay, Northumberland 25 Nov 79
RY/YM ♀	(1974)	Oct 74		
RG/YM ♀	(1974)	Nov 75	Mar 76	
BM/WY ♀	1975			Territory at Newton, Northumberland 76 & 77
GY/BM ♂	1975			Probably stayed 75-76 winter
GW/BM ♂	1975		Mar 76	
GB/BM ♀	1975		Mar 77	White Sands,E. Lothian 21 Feb 79
RW/BM	1975	Oct 76	Mar 77	Largo Bay, Fife 28 Oct 78
YR/YM ♂	(1975)	Aug 75	Feb 76	
YG/YM ♂	(1975)	Oct 75	Feb 76	
GR/YM ♀	(1975)	Oct 75	Apr 76, Mar 77	
GY/YM ♂	(1975)	Aug 75, Aug 76	Mar 76, Mar 77	
YW/YM ♂	(1975)	Sept 75	Mar 76, Mar 77	
GW/YM ♀	(1975)	July 75	Apr 76	Whitley Bay, Northumberland 28 Oct 79
WR/YM ♀	(1975)	July 75	Apr 76, Mar 77	
WY/YM ♀	(1975)	July 75, Sept 76+	Mar 76, Mar77	
WG/YM ♀	(1975)	July 75, Aug 76		
WB/YM ♀	(1975)	July 75, July 76	Apr 76, Mar 77	
RB/YM ♂	(1975)	Oct 75	Feb 76	
YB/YM ♂	(1975)	Aug 75, July 76	Apr 76	
YO/BM ♂	1975	Aug 75	May 76	
WO/BM ♂	1975	July 75, Aug 76	Apr 76	
OW/BM ♀	1975	Sept 75	Apr 76	
RB/BM ♂	1975	July 75, Oct 76		Territory at Newton, Northumberland 1976-1979
BY/BM ♀	1975	July 76	Mar 76	
BG/BM ♂	1975	July 75, Aug 76	Apr 76, Mar 77	
BW/BM ♀	1975	Aug 75, Aug 76	Mar 76	
OR/YM ♂	1975	Sept 75	Mar 76	
RB/MB	1975	Sept 75		
RW/MB	1975	Aug 76	Mar 76	
RO/MB	1975	Aug 75, Sept 76+	Feb 76	
YR/MB	1975	Aug 75		
YW/MB	1975	Aug 75		
YO/MB	1975	Sept 75		

Table continued overleaf

TABLE 26. CONTINUED

Individual	Year of hatching (or ringing	Month of last sighting in autumn	Month of first sighting in spring	Observations away from Lindisfarne & Notes
YR/OM	1976	Sept 76+		
YG/OM	1976	Aug 76	Mar 77	
WY/OM ♂	1976	Sept 76+	Feb 77	
WR/OM	1976	Aug 76		
OY/OM	1976	July 76		
OW/OM	1976	July 76	Mar 77	Boulmer, Northumberland July 77 Tyninghame, E. Lothian 29 Mar 80
WG/OM	1976	Sept 76+		
RW/MY	(1976)	Sept 76+		
RB/OM	1976	Aug 76		
YB/OM	1976	Sept 76+		
GB/OM	1976	Sept 76+		
WB/OM	1976	Aug 76		
BR/OM	1976	Sept 76+		
BO/OM	1976	Sept 76+		
BY/OM ♂	1976	Aug 76	Mar 77	
OB/OM	1976	Aug 76		
BW/OM	1976	Aug 76		
WO/MO	1976			Probably wintered 76-77; Teesmouth, Cleveland 17 Mar 78
YW/MO	1976	Aug 76		Craster, Northumberland 13 Nov 76
BY/MO	1976			Tyninghame, East Lothian 29 Mar 80
WB/MO	1976	Aug 76		
OB/MO	1976	Aug 76	Mar 77	
GB/MO	1976	Sept 76	Mar 77	
W/MO	1976(at Beadnall, Northumb-land)			Tyninghame, East Lothian 16 July 78
BW/MR	1977			Probably wintered 77-78
YR/RM	1977			Dunglass, East Lothian 28 Jan 79
RY/MW	1978			North Berwick, East Lothian 13 Jan 79
OG/RM	1977			Tyninghame, East Lothian 3 July 79
OR/MRO	1979			Hest Bank, Morecambe, Lancs 9 Mar 80

feeding time - at least in the later half of the pre-fledging period - (Figs 9, 10, 13, 14); and the fact that those chicks that did not survive were probably lost to predators and not by starvation . (Indeed, those chicks lost had generally shown similar growth rates to other members of their broods, as found also for Dunlins, in which species mortality of chicks is also due to weather or predation (e.g. Holmes 1966). (This contrasts with the greater variation in growth rates within a brood in some other precocial species, e.g. Coot *Fulica atra* (Visser 1974), terns *Sterna* spp. (Dunn 1975, LeCroy & Collins 1972), gamebirds (Ricklefs 1968), and the large variations of altricial young (e.g. Lack & Lack 1951, Lack 1954, Owen 1960, Ricklefs 1968)). The situation could, however, be different in very windy or wet summers.

Apart from such weather-induced reductions in availability, food appeared to be superabundant in both of the present study areas. The young clearly did not require particular types of prey: whilst small flies were undoubtedly the most typical component, small spiders, sandhoppers, insect larvae, small intertidal worms and small intertidal snails were important prey in some situations. Although parent birds appeared to take a wider range of prey than chicks at both Mestersvig and Lindisfarne, there was undoubtedly great overlap between the diets of the two age-classes.

While the 'off-duty' adult tended to feed a little distance (rarely more than 100 m and usually much less) from the rest of the family, this was probably not to avoid prey depletion since adults and young, and often prey animals also, were mobile. It may, however, have reduced immediate interference in feeding, and provided a vantage point away from the brood from which to detect potential predators and give alarm calls (cf Lenington 1980). Young tended to feed further apart from each other and from the attendant parent as they grew older but it is not known whether this was to avoid interference or simply the result of greater mobility. At Mestersvig, migrant juveniles tended persistently to approach broods of chicks and attempted to feed near them but were continually chased away by the parents, as were other shorebirds. This behaviour by the parents could be adaptive, to reduce feeding interference or to reduce the conspicuousness of a gathering of birds to potential predators. However, both possibilities seem unlikely, the former because of high prey availability and the

latter in view of the conspicuousness of the chasing behaviour itself. Possibly, the chasing is a remnant of early territorial behaviour.

The young appear to be dependent on their parents for warmth until they are about 10 days old and progressively less for up to a week after this. In a detailed laboratory and field study on energetics of chicks, the effects of brooding and the development of insulation by plumage of Ringed Plover, Keskpaik *et al.* (1970) also found that chicks became thermally independent at about 10 - 15 days. It is around this age also that food intake probably reached a plateau level when expressed as a multiplier of BMR (Table 10; cf Paper 1, Koskimies 1962). Before this age thermoregulatory ability fell with falling ambient temperature and was almost non-existent before about 5 days (Keskpaik *et al.* 1970). The duration of periods in which the chicks were not brooded (mainly while they fed) were matched to the rate of fall of body temperature of chicks and this to age, temperature, and time of day. In my study I noticed that, in the low temperatures at Mestersvig, young chicks were brooded almost whenever they stopped feeding, whereas at Lindisfarne periods when the chicks were neither feeding nor being brooded were common earlier. Part of this difference was due, however, to more frequent disturbance by potential predators and humans at Lindisfarne.

The onset of thermoregulation occurred much later than in several other taxa of precocial or semi-precocial birds, such as gulls and ducks, but at about the same age as in the gamebirds (Dunn 1976, Koskimies & Lahti 1964), presumably the result largely of the small size of young waders and gamebirds, giving rise to high surface area:volume ratios and to thin plumage (Koskimies & Lahti 1964, Lasiewski & Dawson 1967, Kendeigh 1970). Thus, the precocity and self-feeding of young shorebirds, apart from removing the need for food-delivery journeys by adults (and the risk of a long period spent in a fixed nest in open habitat), also removes the need for one adult to remain at the nest to brood, this being possible in short spells on the feeding grounds. Chappell (1980) reported that shorebird chicks are particularly tolerant of chilling, and concluded that this was a further adaptation to allow efficient self-feeding. It is also important in areas where there is a high degree of disturbance and may account in part for the maintenance

of fairly high chick survival rates even in sites frequented by humans.

In Greenland, most chicks are moved away from the nest very soon after hatching. Because of asynchrony in hatching this often led to splitting of the brood (or eggs and brood) on the day of hatching between two parents several hundred metres apart, one attending mobile young and the other eggs and/or newly hatched young in the nest scrape. One of the family parties watched at Mestersvig was separated in this way for about one day before reuniting. Such asynchrony in hatching has been reported for Ringed Plovers also by Krechmar (1966) and appears to be fairly widespread in arctic waders (e.g. Dotterel *Charadrius morinellus* - Pullianen 1970; Dunlin - Holmes 1966; Turnstone *Arenaria interpres* - Nettleship 1973). Presumably the development of hatching synchrony is achieved by delays to the older chick and speeding of development of the younger. This would involve costs at least to the older chicks in terms of a prolonged high risk period in the nest and delayed start of feeding, as well as benefits to the younger chicks, and to the parent in terms of increased chick production and reduced parental work. Also the strategy of Ringed Plovers to leave nests and perform distraction displays when predators are in the vicinity, rather than sitting tightly and relying on camouflage, may lead to increased asynchrony in hatching (see Norton 1972, Pitelka, Holmes & MacLean 1974, Hunter, Ross & Ball 1976).

At Lindisfarne most of the feeding by chicks, at least for the first few days after hatching, occurs on territory and often close to the nest so that splitting of broods is less marked, involving at most only a few metres. The need to move at Mestersvig appears to be due to the rapidly changing microclimate as each area progressively dries out after emerging from the snow. Thus, in early August, the damp sparsely-vegetated areas near the shore at Noret held higher densities of active small flies than many other nearby areas which were exposed earlier and had dried and which also had more vegetation giving cover to the flies, especially in wind (see Greenwood 1978). This variation in state of ground and availability of prey is the probable reason for the early desertion of territories and movement of the broods at Mestersvig. In contrast, at Lindisfarne, little consistent change was apparent in prey availability, even in a small area, over much of the

summer (Appendix 5).

Intervals between brooding were somewhat temperature-dependent only during the first 10 days of chick growth, but the total time spent feeding in each 6 h period was related to temperature throughout much of the pre-fledging period in Greenalnd. The feeding rate in Greenland showed a relationship with temperature (Table 7 & Appendix 4) which matched variation with temperature in the activity of the prey animals - small flies and spiders (Greenwood 1974b, 1978). Thus feeding appeared to be concentrated at the times when prey was most available. This also resulted in the strong diurnal pattern (Fig. 9 & Appendix 4). At Lindisfarne, temperatures, which were generally higher than in Greenland, did not influence feeding time or feeding rate but both the latter were depressed by rain (which also affected feeding rate and activity at Mestersvig) and strong winds, again indicating a concentration of feeding activity when this was most profitable. Flies were a main prey at Lindisfarne and their activity appeared to be depressed by rain and wind. Wet weather also depressed the activity of prey animals at Mestersvig (Greenwood 1974b). Such conditions may also depress the detectability of prey and the efficiency of foraging movements (Table 11 & Paper 2). Although, at Lindisfarne, insect activity appeared to be depressed at night, the activity of sandhoppers, the other main prey of the birds, was maximal at that time. The activity of some intertidal invertebrates which may also be included in the diet is also enhanced at night (Paper 2). This may account for the lack of a diurnal rhythm in foraging activity at Lindisfarne.

Development of foraging behaviour and its influence upon survival

In the first hours after leaving the nest, chicks made brief 'feeding' excursions and appeared to peck at various items, both suitable and unsuitable as prey; but suitable prey appeared to dominate within the first day. Foraging success and rate of taking prey increased progressively, in subsequent days. An increase in waiting and giving-up times with age was apparent and each pause became more likely to result in a peck. This may be related to an improving ability to recognise suitable cues and/or to greater selectivity. The constancy of handling time, despite increasing prey size, indicates progressive improvement in handling ability with age. Similarly, the number of

paces moved to take prey did not change despite an increase in pace length, so that the range at which prey were taken must have increased. The frequency of 'down' waiting positions decreased with age, this decrease possibly continuing for some time after fledging. This may reflect an increasing ability to react and orient to cues rapidly from a distance without the need for a 'second look'.

Food intake appeared to be less than energy expenditure in the first day or two after hatching, as weight fell in this time and yolk reserves were used up, but weights recovered from about the third day, as found also by Keskpaik *et al.* (1970). The changes with age of the estimated daily intakes agree with this (Table 10). Presumably adverse weather could be particularly critical in the first few days after hatching. As discussed earlier, however, losses due to inadequate food supply throughout the rest of the pre-fledging period seem unlikely.

For much of the time one adult was close to or brooding the young and each adult did most of its feeding while 'off-duty' some distance away (but well within sight and alarm-call range). As in Spotted Flycatchers *Muscicapa striata* (Davies 1976) and Sandwich Terns *Sterna sandvicensis* (Dunn 1972), the improvement in foraging performance appeared to be the result of growth and experience rather than of copying from adults, unlike in the Oystercatcher *Haematopus ostralegus* (Norton-Griffiths 1969) and Ring Dove *Streptopelia risoria* (Wortis 1969).

By the time of fledging, feeding rates and foraging behaviour of young were very similar to those of adults, and this remained true throughout the early autumn (Table 13), although young birds tended to feed for longer, presumably as growth continued then (Paper1). In late autumn and winter, however, there were indications that the rate of food intake of young was less than that of adults (Table 13), when prey became less available in the adverse conditions (Paper 2).

Groves (1978) found that juvenile Turnstones on migration in Massachussetts in mid-July to October pecked and took prey significantly less frequently than did adults, although the proportions of pecks which were successful were similar. Juveniles also tended to be subordinate to adults in aggressive interactions on the feeding grounds.

Lower feeding success by juveniles than adults at times of food scarcity were reported for Cattle Egrets *Ardeola ibis* in South Africa (Siegfried 1971, 1972). Brown Pelicans *Pelecanus occidentalis*, 18-24 months old, also miss prey on a higher percentage of dives than do adults (Orians 1959). Dunn (1972) found that adult Sandwich Terns caught more fish per unit time than first winter birds, by diving from greater heights, but on occasions of superabundance of small fish near the tideline, rates became similar for the two age groups. Recher & Recher (1969) reported lower feeding success and food intake in younger Little Blue Herons *Florida caerulea* (up to about one year old) than in older birds and argued that this resulted in higher mortality in winter and early spring. They also cited unpublished work by D. Williard indicating that two-year-old Caspian Terns *Hydroprogne caspia* miss prey more often and forage longer each day than adults. Norton-Griffiths (1967,1969) found that some young Oystercatchers may rely in part on parental feeding for over 30 weeks after hatching, if feeding on *Carcinus* or *Mytilus*. Indeed, they may take three years to become as efficient as adults at feeding on Mussels *Mytilus edulis*. In flocks of Woodpigeons *Columba palumbus*, subordinate birds, including many young, feed at the front edge of flocks and are less successful. This appears to be due to inexperience in selecting the food which can be eaten most efficiently, and such (i.e. subordinate) young birds suffer higher mortality during unfavourable seasons (Murton, Isaacson & Westwood 1971).

Parent birds of most of the species cited above feed their young, in some cases even after fledging. In contrast, most shorebirds never receive food from their parents, and thus must be able to feed effectively by the time that the yolk reserve is used up (within the first few days). This may be possible only in areas of superabundance of obvious mobile prey, in most cases adult Diptera. In arctic areas, such superabundance may occur only in rapidly varying localities, such as the wet areas which accompany the receding snow melt in NE Greenland. This reinforces Holmes' (1966) suggestion that precociality may be particularly advantageous in the Arctic in that the young are able to move, sometimes long distances, to locally favourable feeding sites. This movement may be even more marked in Ringed Plovers than in some other species, as they nest on the barren gravels which are the first flat lands to emerge from snow cover but also the first to dry out.

This adaptation to early movement away from the nesting site allows the wide breeding distribution in NE Greenland where Ringed Plover is the commonest wader. On the wintering grounds, as adverse weather conditions develop in autumn and winter, food demands increase, prey becomes less available and is often detectable only by brief subtle cues (Papers 1 & 2). At these times, adult/juvenile differences in feeding ability are revealed again.

There is evidence that juvenile waders of some species occur on their first autumn migration mainly in different habitats to adults; or that they may roost on the fringes of main flocks or in smaller roosts (Pienkowski 1975, Pienkowski & Dick 1976, W.J.A. Dick unpublished), but it is not known if this is due to competitive exclusion. This situation contrasts with that in geese where families remain together over the winter, and where adults appear to remain more alert for predators while their young feed faster than when alone(e.g. Owen 1972).

The period in late autumn and winter when differences in foraging between age categories of birds could be detected (implying difficulty in feeding for at least some juveniles) coincided with the period when most of those birds which left Lindisfarne for part of the year were absent. Why some individuals stay and others leave is, however, unknown; nor is it known whether differences occur within broods or only between broods.

The possible advantages to staying seem to be:-

1. Young birds do not have to learn suddenly to feed on a new type of habitat or prey. Young birds newly arrived in early autumn in NW Africa were frequently seen trying to feed in unsuitable situations (Pienkowski 1975, Dick 1976, Dick & Pienkowski 1979). Resident Ringed Plovers may even learn the cues given by potential winter foods before fledging, as at Lindisfarne.
2. Apart from habitat differences, the birds do not have to learn the characteristics of particular new sites.
3. Individuals (especially young ones soon after fledging) are not subject to the risks of migration and the need to feed sufficiently to deposit fat reserves for this. This may allow a late end to the breeding season and thus an increased potential production of young.

4. The birds do not have to fit their moult into a migration schedule (cf Pienkowski *et al.* 1976).
5. Resident birds are present to take up territories as soon as conditions are suitable.

The main disadvantage appears to be that resident birds are subject to a harsher climate, on average, and consequent reduced prey availability in some months or years than those which move south. Perhaps the risks and benefits of the two strategies are fairly similar at Lindisfarne so that both co-exist, but data to test this are very difficult to obtain. Feeding observations are available in October (the last month when many potential migrants were present) from three colour-ringed individuals known to have stayed at Lindisfarne (22 observation sessions totalling 44 min) and 13 thought to have departed later that autumn (20 totalling 34 min). Some differences in feeding rates and behaviour were found, these tending only to border on the 5% significance level, partly because of small sample sizes (Table 27). Individuals which were to stay pecked more frequently than those which departed and took more worms (but neither difference was statistically significant). More of the departers' pecks were of small prey ($P = 0.016$) whereas the stayers took more unidentified prey ($P = 0.04$) - these tending to be larger than "small items" - and made more pecks of unknown outcome ($P = 0.004$). Both the mean waiting time and mean 'giving-up' time of stayers were shorter than of departers but only significantly so when considered together. The stayers had more successful waits (but not significantly so). If real, these differences could mean either that stayers were detecting more prey or were being less selective. The suggested differences in rates of prey taken suggest the former to be more likely.

Thus, these data are compatible with the idea that those birds which stay at Lindisfarne are the better feeders; but the data are inadequate to test this critically. They are also insufficient to ascertain whether birds from one brood tend to behave similarly. From one brood of three ringed in 1974, two stayed for the winter and one was not seen between mid October and early March. One bird of this brood was recorded as wintering at Lindisfarne in its first, second and third winters.

TABLE 27. COMPARISON OF FEEDING OBSERVATIONS MADE AT HOLY ISLAND SANDS IN OCTOBER BETWEEN RINGED PLOVERS WHICH LEFT LINDISFARNE FOR THE WINTER AND THOSE WHICH STAYED. GIVEN AS MEAN ± S.E. (n)

	Leavers	Probability level of t test	Stayers
Total time of observations (min)	34		44
Total pecking rate (min^{-1})	13.5 ± 1.0 (20)	0.163	15.5 ± 1.0 (22)
Estimated rate of taking thin worms (min^{-1})	8.3 ± 0.6 (20)	0.084	9.7 ± 0.6 (22)
Estimated rate of taking unidentified prey (min^{-1})	0.11 ± 0.09(20)	0.040*	0.97 ± 0.38(22)
Estimated rate of taking small items (min^{-1})	3.6 ± 1.2 (20)	0.016*	0.3 ± 0.1 (22)
Rate of making pecks of unknown outcome (min^{-1})	7.1 ± 1.0 (20)	0.004**	11.5 ± 1.0 (22)
Rate of successful waits (ups followed by pecks with or without intervening run) (min^{-1})	12.4 ± 0.7 (15)	0.071	15.3 ± 1.3 (16)
Rate of unsuccessful waits (up followed by run to new up) (min^{-1})	4.9 ± 0.6 (15)	0.421	5.6 ± 0.6 (16)
Mean 'giving up time' (sec)	2.3 ± 0.2 (15)	0.513	2.2 ± 0.2 (16)
Mean 'waiting time' (sec)	2.1 ± 0.1 (15)	0.061	1.9 ± 0.1 (16)
Mean 'giving up' or 'waiting' time (sec)	2.2 ± 0.1 (15)	0.050*	1.95 ± 0.1 (16)

Weights of juvenile Ringed Plovers tend to be lower than those of adults during the winter (Eades & Okill 1976, McGregor & Jones 1979), suggesting that they may be less able to maintain condition (e.g. Evans & Smith 1975, Pienkowski, Lloyd & Minton 1979, Dick & Pienkowski 1979, Davidson 1979, Pienkowski 1980). Apparent (minimum) survival of young from fledging to one year old was less than that of adults (Tables 17, 19, 20). The survival, from hatching to one year old, of Ringed Plovers at Lindisfarne (45% x 59% = 27%) is notably similar to the approximate estimate obtained by indirect means for Dunlin in Finland of 27.5% (from Soikelli 1970b). Presumably lack of experience in foraging techniques or the ability to discover by sampling areas of best feeding may be involved in this difference between adults and young.

More surprisingly, the apparent survival from one to two years old (57%) was similar to that from fledging to one year (59%) and much less than that of older birds (80+%). Although it is possible that the lower apparent survival of young birds results from lower site fidelity, this is unlikely to represent more than a small fraction of the difference as good coverage was achieved over much of the coast of NE England and SE Scotland and those birds which were found elsewhere were mainly at the nearest concentrations of Ringed Plovers both to the north and the south. In the related and ecologically similar Piping Plover *C. melodus*, Wilcox (1959), in a large scale ringing study in New York State, found very few movements away from the nesting area in later years. The tendency for birds to settle mainly near their site of hatching, but for a few to disperse widely, seems similar to that found for Dunlin by Soikelli (1970a) and for many - but not all - wader species reviewed in that work.

The return of birds to the breeding grounds at one year old is common in small waders, although the return tends to be delayed one or more years in larger species (e.g. Harris 1967, Johnson 1973, Dare & Mercer 1974, Minton 1975, Pienkowski & Knight 1975, Glutz *et al.* 1975, 1977, Pienkowski *et al.* 1976, Pienkowski & Knight 1977, various sources reviewed by Pienkowski in press). This may imply some risk in breeding at one year, which is less in small birds (which may also have behaviour adapted to shorter lives).

Lower survival rates of birds in their first year are common (see, e.g. Lack 1943 and, for waders, Boyd 1962). Evidence for lower survival in the second and third years than in later years is less frequent, partly because the data are rarely available, although evidence for gradual improvement in breeding performance with age is more common (e.g. Coulson & White 1958). Soikelli (1970b) found a slight but not significant decrease in apparent survival rate of Dunlins in Finland between one and two years after ringing before an increase in rate in later years, and remarked on the apparent tendency for survival rate to increase slightly with age. Grosskopf (1959), studying Redshanks *Tringa totanus* ringed at adults at a German breeding colony, found that the apparent survival rate increased in successive years and argued that the adult death-rate decreased with age from 30%, through 23% to 18% in the three years. Boyd (1962) pointed out, however, that the apparent increase in survival could also be due to an increasing tendency to return to the same breeding place with experience in breeding. Kortlandt (1942) found progressivly increasing annual survival in first-year, second-year, third-year and adult Cormorants *Phalacrocorax carbo* in the Netherlands. Boyd (1962) found indications that the survival of Avocets *Recurvirostra avosetta* was lower in the fourth and fifth years (48-56%) than in the second and third (67%) and suggested that this may result from an increase in mortality at first breeding at three years old. However, the apparent difference in this case may also have arisen from ring loss, which was a serious problem with the aluminium rings used in these earlier studies and remains so, for some species at least, even with the newer, harder metal substitutes (e.g. Harris 1980, Clapham 1978). This is presumably at least a contributory reason for the low apparent survival rates calculated by Boyd (1962) and similar studies based on ringing returns compared with detailed studies of returns to a study site (see Grosskopf 1964, Soikelli 1970b, Harris 1980). For Ringed Plovers, Boyd calculated an adult survival of only 58% using ringing results compared with 80-90% in the present study. Laven (1940) in a study at one site in N. Germany also calculated a low annual survival rate of 59%, but Grosskopf (1964) estimated 70-75%. Similarly studies of return to breeding site of Dunlins have given annual survival rates of 75% and 71% compared with 61% and 62% from ringing recoveries (Soikelli 1970b, also citing Martin-Lof 1955, Boyd 1962, Holmes 1965). For

Oystercatchers, intensive studies of returns of birds have given annual survivals of 93% (Grosskopf 1964) and 89% (Harris 1967), while Boyd's (1962) estimate using ringing recoveries was only 71%. Survival rates and populations dynamics of Ringed Plovers are considered further in Paper 4.

SUMMARY

The food, foraging behaviour, growth and survival of Ringed Plover chicks were studied in 1974 at Mestersvig, NE Greenland, and from 1973 to 1976 at Lindisfarne, NE England. Post-fledging survival, dispersal and recruitment were also investigated for the Lindisfarne population.

Growth rates were similar in both study areas and comparable to those reported from other sites. A diurnal rhythm in feeding activity was more evident in the Arctic than at temperate latitudes despite continuous daylight in the former area. This was correlated with low nocturnal temperatures and prey availability. Brooding decreased progressively during the pre-fledging period; the relationship of brooding period to age, environmental conditions and area were investigated.

Small Diptera were the main prey both in the tundra study area in Greenland and on the sea-shore at Lindisfarne, where sandhoppers and some intertidal invertebrates also were taken. Food intake rate increased with age. Estimates of minimum calorific intake in relation to age are presented for birds at Mestersvig. Detailed changes in foraging behaviour with age and environmental conditions at Lindisfarne are described.

Survival from hatching to fledging varied between 40% and 60% in different areas and years, and at least 59% of birds survived from fledging to about one year old. Minimum survival from one to two years old was only 57% but year to year survival of older birds was higher, that of breeding adults being at least 80%. Most birds returned to the breeding area and attempted to breed when one year old. The extent of dispersal from Lindisfarne, and the wintering areas of the Lindisfarne-breeding birds are investigated.

It is concluded that food supply did not limit growth or chick survival in either study area. The appropriateness of adaptations of Ringed Plover feeding and brooding behaviour for arctic and temperate nesting are discussed. Food availability and foraging ability may influence survival of young in later autumn and winter. The alternative strategies of residency and migration are discussed in relation to Lindisfarne Ringed Plovers, as are the age-related variations in survival rates.

REFERENCES

Armstrong, E.A. 1954. The behaviour of birds in continuous daylight. *Ibis* 96: 1-30

Asbirk, S. & Franzmann, N.-E. 1978a. Studies of Snow Buntings. pp 132-142 in Green & Greenwood (1978).

Asbirk, S. & Franzmann, N.-E. 1978b. The diurnal rhythm of Wheatears in continuous daylight. pp 144-148 in Green & Greenwood (1978).

Boyd, H. 1962. Mortality and fertility of European Charadrii. *Ibis* 104: 368-387

Buxton, E.J.M. 1939. The breeding of the Oystercatcher. *Brit. Birds* 33: 184-193

Brewer, R. & Harrison, K.G. 1975. The time of habitat selection by birds. *Ibis* 117: 521-522

Chappell, M.A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. *Comp.Biochem.Physiol.* 65A: 311-317

Clapham, C. 1978. Ring wear on Turnstones. *Wader Study Group Bull.* 23: 32

Dare, P.J. & Mercer, A.J. 1974. The timing of wing-moult in the Oystercatcher *Haematopus ostralegus* in Wales. *Ibis* 116: 211-214

Davidson, N.C. 1979. Changes in the body composition of shorebirds during winter. *Wader Study Group Bull.* 26: 29-30

Davies, N.B. 1972. Parental care and the transition to independent feeding in the young Spotted Flycatcher (*Muscicapa striata*). *Behaviour* 59: 280-295

Dick, W.J.A. (Ed.) 1976. *Oxford & Cambridge Mauritanian Expedition 1973 Report.* Cambridge

Dick, W.J.A. & Pienkowski, M.W. 1979. Autumn and early winter weights of waders in north-west Africa. *Ornis Scand.* 10: 117-123

Dorst, J. 1974. *The Life of Birds.* Vol. 2. Weidenfeld & Nicolson, London

Dunn, E.H. 1976. The development of endothermy and existence energy expenditure in Herring Gull chicks. *Condor* 78: 493-498

Dunn, E.K. 1972. Effect of age on fishing ability of Sandwich Terns (*Sterna sandivicensis*). *Ibis* 114: 360-366

Dunn, E.K. 1975. The role of environmental factors in the growth of tern chicks. *J.Anim.Ecol.* 44: 743-754

Eades, R.A. & Okill, J.D. 1976. Weight variations of Ringed Plovers on the Dee Estuary. *Ringing & Migration* 1: 92-97

Evans, P.R. & Smith, P.C. 1975. Studies of shorebirds at Lindisfarne, Northumberland. 2. Fat and pectoral muscle as indicators of body composition in the Bar-tailed Godwit. *Wildfowl* 26: 64-76.

Ferns, P.N. 1978a. Ecological distribution of wading birds. pp 79-84 in Green & Greenwood (1978)

Ferns, P.N. 1978b. General observations of mammals. pp 164-167 in Green & Greenwood (1978).

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. (Eds.) 1975, 1977. *Handbuch der Vogel Mitteleuropas*, Vols. 6, 7. Akademische Verlagsgesellschaft, Weisbaden

Green, G.H. 1978a. The census of waders. pp 84-109 in Green & Greenwood (1978)

Green, G.H. 1978b. Discussion of wader measurements and migrations. pp 61-68 in Green & Greenwood (1978).

Green, G.H. & Greenwood, J.J.D. (Eds.) 1978. *Joint Biological Expedition to North East Greenland 1974*: the report of the joint expedition comprising Wader Study Group NE Greenland Expedition 1974 and Dundee University NE Greenland Expedition 1974. Dundee University NE Greenland Expedition, Dundee

Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. *J.Zool., Lond.* 183: 311-328

Green, G.H., Pienkowski, M.W., Brown, S.C., Ferns, P.N. & Mudge, G.P. 1978. Methods used for wader studies. pp 38-51 in Green & Greenwood (1978)

Greenwood, J.J.D. 1974a. Energy content of some tundra arthropods and plant propagules. p 85 in O'Brien & Greenwood (1974)

Greenwood, J.J.D. 1974b. The distribution and activity of tundra arthropods. pp 48-55 in O'Brien & Greenwood (1974)

Greenwood, J.J.D. 1978. Activity patterns and habitat distribution of tundra invertebrates. pp 168-182 in Green & Greenwood (1978)

Grosskopf, G. 1959. Zur Biologie des Rotschenkels (*Tringa t. totanus*). II. *J.Orn.* 100: 210-236

Grosskopf, G. 1964. Sterblichkeit und Durch schnittsalter eineger Kustenvogel. *J.Orn.* 105: 427-449

Groves, S. 1978. Age-related differences in Ruddy Turnstone foraging and aggressive behaviour. *Auk* 95: 95-103

Harris, M.P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. *Ibis* 109: 180-193

Harris, M.P. 1980. Loss of weight and legibility of bird rings. *Ringing & Migration* 3: 41-48

Heppleston, P.B. 1972. The comparative breeding ecology of oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. *J.Anim.Ecol.* 41: 23-51

Holmes, R.T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. *Condor* 68: 3-46

Hunter, R.A., Ross, H.A. & Ball, A.J.S. 1976. A laboratory simulation of predator-induced incubation interruption using ring-billed gull eggs. *Can.J.Zool.* 54: 628-633

Johnson, O.W. 1973. Reproductive condition and other features of shorebirds resident at Eniwetok Atoll during the boreal summer. *Condor* 75: 336-343

Karplus, M. 1952. Bird activity in the coninuous daylight of the arctic summer. *Ecology* 33: 129-134

Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72: 60-65

Keskpaik, J., Ivanova, N., Keskpaik, T. & Kallis, A. 1970. The factors determining the structure of stereotypic behaviour of the family groups of *Charadrius h. hiaticula* L. *Eesti NSV Teaduste Akadeemi Toimetised. Biologia.* 19: 195-210 (In Russian)

Kortlandt, A. 1942. Levensloop samenstelling en structur der Nederland se aalocholverbevolking. *Ardea* 31: 175-280

Koskimies, J. 1968. Ontogeny of thermoregulation and energy metabolism in some gallinaceous birds. *Trans. 5th Congr. Intern. Union of Game Biologists, Bologna.* pp 149-160

Koskimies, J. & Lahti, L. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of European ducks. *Auk* 81: 281-307

Kozlova, E.V. 1961. Charadriiformes. *Fauna SSR, Ptitsy 2.* Akad. Nauk SSSR, Moscow & Leningrad

Krechmar, A.V. 1966. The birds of the western parts of the Taimyr Peninsula. *Trudy Zool. Inst. Leningrad* 30: 185-312 (In Russian)

Lack, D. 1943. Do juvenile birds survive less well than adults? *Brit. Birds* 39: 258-264

Lack, D. 1954. *The Natural Regulation of Animal Numbers.* University Press, Oxford

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds.* Methuen, London

Lack, D. & Lack, E. 1951. The breeding biology of the Swift *Apus apus*. *Ibis* 93: 501-546

Lasiewski, R.C. & Dawson, W.R. 1967. A re-examination of the relationship between standard metabolic rate and body weight in birds. *Condor* 69: 12-23

Laven, H. 1940. Beitrage zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). *J.Orn.* 88: 183-287

LeCroy, M. & Collins, C.T. 1972. Growth and survival of Roseate and Common Tern chicks. *Auk* 89: 595-611

Lenington, S. 1980. Biparental care in Killdeer: an adaptive hypothesis. *Wilson Bull.* 92: 8-20

Lenington, S. & Mace, T. 1975. Mate fidelity and nesting site tenacity in the Killdeer. *Auk* 92: 149-151

Lind, H. 1965. Parental feeding in the Oystercatcher (*Haematopus ostralegus*). *Dansk. Ornith. Foren. Tiddskr.* 59: 1-31

Maher, W.J. 1964. Growth rate and development of endothery in the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*) at Barrow, Alaska. *Ecology* 45: 520-528

Martin-Lof, P. 1961. Mortality rate calculations on ringed birds with special reference to the Dunlin (*Calidris alpina*). *Ark.Zool.* 13: 483-491

McGregor, H.M. & Jones, H.M. 1979. Wader weights. pp 64-68 in N.J.B.A. Branson (Ed.) *Wash Wader Ringing Group Report 1977-1978*

Minton, C.D.T. 1975. The Waders of the Wash - ringing and biometric studies. Report of Scientific Study G, Wash Water Storage Scheme Feasibility Study to the Natural Environment Research Council.

Murton, R.K., Isaacson, A.J. & Westwood, N.J. 1971. The significance of gregarious feeding behaviour and adrenal stress in a population of wood-pigeons *Columba palumbus*. *J.Zool., Lond.* 165: 53-84

Nettleship, D.N. 1973. Breeding ecology of Turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. *Ibis* 115: 202-217

Norton, D.W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. *Condor* 74: 164-176

Norton-Griffiths, M. 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher on the Edible Mussel. *Ibis* 109: 412-424

Norton-Griffiths, M. 1969. The organisation, control and development of parental feeding in the Oystercatcher (*Haematopus ostralegus*). *Behaviour* 34: 55-114

O'Brien, R.M.G. & Greenwood, J.J.D. (Eds.) 1974. *Report of the University of Dundee North East Greenland Expedition 1972.* Dundee

O'Connor, R.J. 1977. Differential growth and body composition in altricial passerines. *Ibis* 119: 147-165

Orians, G.H. 1969. Age and hunting success in the Brown Pelican (*Pelecanus occidentalis*). *Anim.Behav.* 17: 316-319

Owen, D.F. 1960. The nesting success of the Heron *Ardea cinerea* in relation to the availability of food. *Proc.zool.Soc.Lond.* 133: 597-617

Owen, M. 1972. Some factors affecting food intake and selection in white-fronted geese. *J.Anim.Ecol.* 41: 79-92

Pienkowski, M.W. (Ed.) 1975. *Studies on coastal birds and wetlands in Morocco 1972.* Joint report of the University of East Anglia Expedition to Tarfaya Province, Morocco 1972 and the Cambridge Sidi Moussa Expedition 1972. Norwich

Pienkowski, M.W. 1980. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Proc. IWRB Feeding Ecology Symp., Gwatt, Switzerland, September 1977. *Verh.Orn. Ges.Bayern* 23 (in press)

Pienkowski, M.W. in press. Chapters on movements of various wader species in S. Cramp & K.E.L. Simmons (Eds.) *The Birds of the Western Palearctic* Vol. 3. University Press, Oxford

Pienkowski, M.W. & Dick, W.J.A. 1976. Some biases in cannon- and mist-netted samples of wader populations. *Ringing & Migration* 1: 105-107

Pienkowski, M.W. & Knight, P.J. 1975. Wing-moult of Oystercatchers in Iceland. *Ibis* 117: 114

Pienkowski, M.W. & Knight, P.J. 1977. La migration postnuptiale des limicoles sur la côte atlantique du Maroc. *Alauda* 45: 165-190

Pienkowski, M.W., Knight, P.J., Stanyard, D.J. & Argyle, F.B. 1976. The primary moult of waders on the Atlantic coast of Morocco. *Ibis* 118: 347-365

Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26: 134-148

Pitelka, F.A., Holmes, R.T. & MacLean, S.F. 1974. Ecology and evolution of social organization in arctic sandpipers. *Amer.Zool.* 14: 185-204

Prater, A.J. 1974. Breeding biology of the Ringed Plover. pp 15-22 in *Proc. IWRB Wader Symp. Warsaw 1973.* Warszawa

Pulliainen, E. 1970. On the breeding biology of the Dotterel (*Charadrius morinellus*). *Ornis Fenn.* 47: 69-73

Ratcliffe, D.A. 1976. Observations on the breeding of the Golden Plover in Great Britain. *Bird Study* 23: 63-116

Recher, H.F. & Recher, J.A. 1969. Comparative foraging efficiency of adult and immature little blue herons (*Florida caerulea*). *Anim.Behav.* 17: 320-322

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis* 110: 419-451

Ricklefs, R.E. 1969. Preliminary models for growth rates in altricial birds. *Ecology* 50: 1031-1039

Rittinghaus, H. 1965. Untersuchungen am Seeregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeoog. *J.Orn.* 97: 117-155

Safriel, U.N. 1975. On the significance of clutch size in nidifugous birds. *Ecology* 56: 703-708

Siegfried, W.R. 1971. Feeding activity of the Cattle Egret. *Ardea* 59: 38-46

Siegfried, W.R. 1972. Aspects of the feeding ecology of cattle egrets (*Ardeola ibis*) in South Africa. *J.Anim.Ecol.* 41: 71-78

Soikelli, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). *Ann.Zool.Fenn.* 4: 158-198

Soikelli, M. 1970a. Dispersal of Dunlin *Calidris alpina* in relation to sites of birth and breeding. *Ornis Fenn.* 47: 1-9

Soikelli, M. 1970b. Mortality and reproductive rates in a Finnish population of Dunlin *Calidris alpina*. *Ornis Fenn.* 47: 149-158

Summers, R.W. 1972. The diurnal rhythm of Snow Buntings in continuous daylight. pp 51-55 in I.H.M. Smart & R. O'Brien (Eds.) *Report of the Dundee University Scoresby Land Expedition 1970.* Dundee

Summers, R.W. 1974. The diurnal pattern of the Snow Bunting. pp 59-60 in O'Brien & Greenwood (1974)

Thomson, A.L. (Ed.) 1964. *A New Dictionary of Birds.* Nelson, London

Tinbergen, N. & Norton-Griffiths, M. 1964. Oystercatchers and mussels. *Brit. Birds* 57: 64-70

Visser, J. 1974. The post-embryonic development of the Coot *Fulica atra*. *Ardea* 62: 172-189

Voous, K.H. 1960. *Atlas of European Birds.* Nelson, London

Welty, J.C. 1962. *The Life of Birds.* Saunders, Philadelphia & London

Wilcox, L. 1959. A twenty-year study of the Piping Plover. *Auk* 76: 129-152

Wilson, J.R. 1978. Agricultural influences on waders nesting on the South Uist machair. *Bird Study* 25: 198-206

Wortis, R.P. 1969. The transition from dependent to independent feeding in the young Ring Dove. *Anim.Behav.Monograph.* 21: 1-54

Paper 4. Aspects of the breeding biology and population dynamics of two populations of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland

INTRODUCTION

The Ringed Plover is a small shorebird breeding over a wide range of latitudes (Fig. 1) from north Greenland (where it is the commonest wader in many areas, e.g. Salomonsen 1950, Larson 1960, Meltofte 1975, Green 1978 - to the shores of Britain and adjacent parts of the western European mainland (e.g. Voous 1960). The range spreads from across the whole of the northern USSR to W. Greenland and the Canadian arctic archipelago, where the species is replaced by the Semipalmated Plover *C. semipalmatus*, sometimes considered to be conspecific (see Smith 1969), and which is also the commonest breeding wader in some areas (Sutton & Parmelee 1955).

In the northern parts of the breeding range the birds nest both inland and near the coast on barren land, such as stony ground and river gravels. At lower latitudes such habitats are generally restricted to the coast and in Britain the species is mainly a coastal nester. Concern has been expressed in recent years that a decrease may have occurred since the 1940's in the numbers and range of Ringed Plovers breeding in Britain, apparently due to increased human disturbance of the coasts (see Parslow 1967, Prater 1976).

Ecology, behaviour and distribution of Ringed Plovers outside the breeding season have been considered by Pienkowski (1980) and in Papers 1 & 2. Many aspects of the breeding behaviour and nesting of Ringed Plovers and the other small European plovers have been described previously, notably by Laven (1940), Edwards, Hosking & Smith (1947), Mason (1947), Simmons (1953, 1955, 1956), Sluiters (1954), Rittinghaus (1956), Walters (1957) and Glutz *et al.* (1975). However, studies on the arctic breeding grounds, which form most of their range, are lacking and, in Britain, no intensive study has been published since concern was expressed about their possible decline.

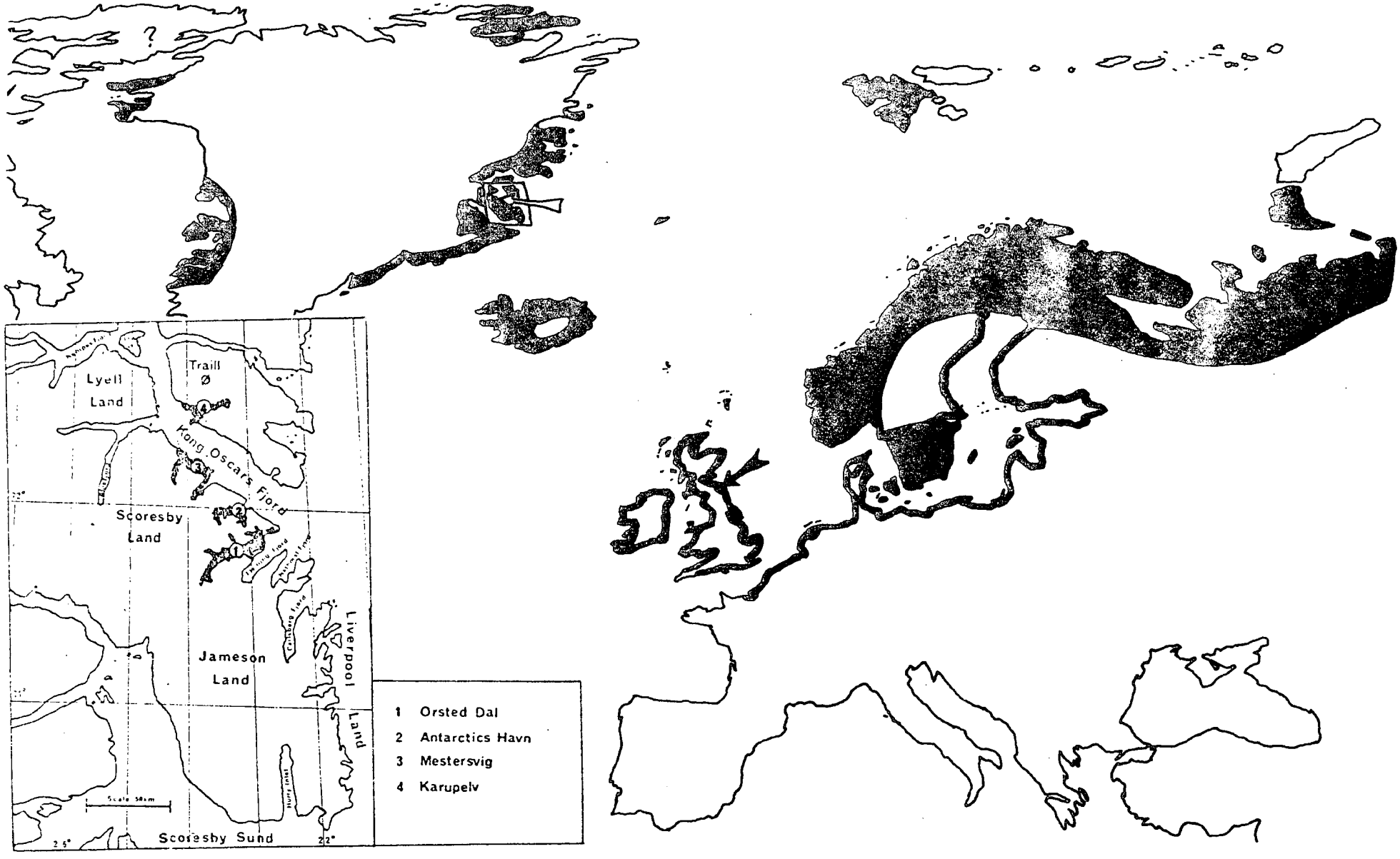


Figure 1. The western part of the breeding distribution of Ringed Plovers according to Voous (1960). Location of main study sites indicated by arrows. Inset is the wider study area in Greenland.

The present paper summarizes information on the nesting of Ringed Plovers at the Lindisfarne National Nature Reserve, Northumberland, in the southern part of the breeding range, and compares this with the situation in Scoresby Land, NE Greenland, well to the north. Together with information on the later stages of the breeding season and subsequent survival of young (already presented in Paper 3), the timing of breeding, population dynamics and breeding distribution are discussed.

STUDY AREAS

Scoresby Land

Observations were made near Mestersvig Government Station, Scoresby Land, NE Greenland (72° 14' N, 23° 55' W) during the Joint Biological Expedition to North East Greenland 1974 from 25 June, at which time the birds were taking up territory and laying, to 16 August, shortly after the first young had fledged. The 1974 season was exceptionally late and some additional less detailed information from other valleys in Scoresby Land (where times of breeding differed - Green, Greenwood & Lloyd 1977), obtained by other members of the Expedition, are also incorporated.

The detailed study area around Mestersvig station (Figs. 1, 2) was mainly 'river-bed' shingle and sparse tundra heath (i.e. 30-60% cover by vascular plants; organic crust of lichen covering ground between heath plants; some disturbance by frost heaving - see Green *et al.* 1978, Green 1978). During the study period, snow cover progressively decreased from greater than 90% on 25 June to about 60% on 6 July and to less than 10% by late July. Generally a damp zone existed in the latest areas from which snow had melted and also in small pools and streams. The shore of the small inlet, Noret, was ice covered until mid-July, after which melt run-off and slight tidal movement gave rise to a damp zone there also. Certain other areas visited in NE Greenland had more vegetation cover but Ringed Plovers tended to occupy the more barren areas (see Green 1978, Ferns 1978).

Northumberland

Studies at Lindisfarne National Nature Reserve (55° 40' N, 1° 50' W) and adjacent parts of the Northumberland coast (Figs. 1 & 3) took place

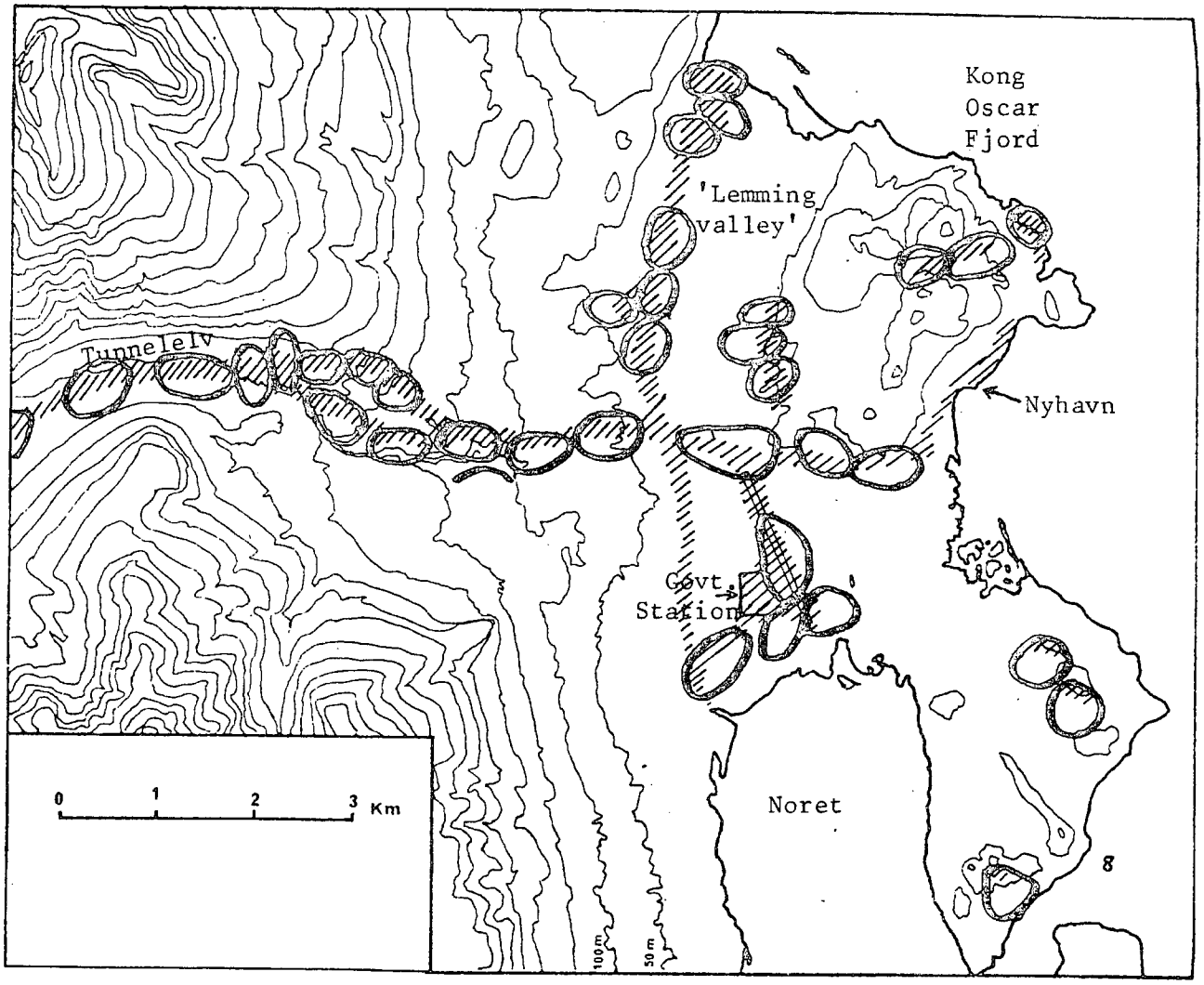


Figure 2. Distribution of Ringed Plover territories (▬) at Mestersvig, showing the areas with snow-free patches in late June (////), consisting mainly of cleared tracks and runway, some steeper slopes and river gravels.

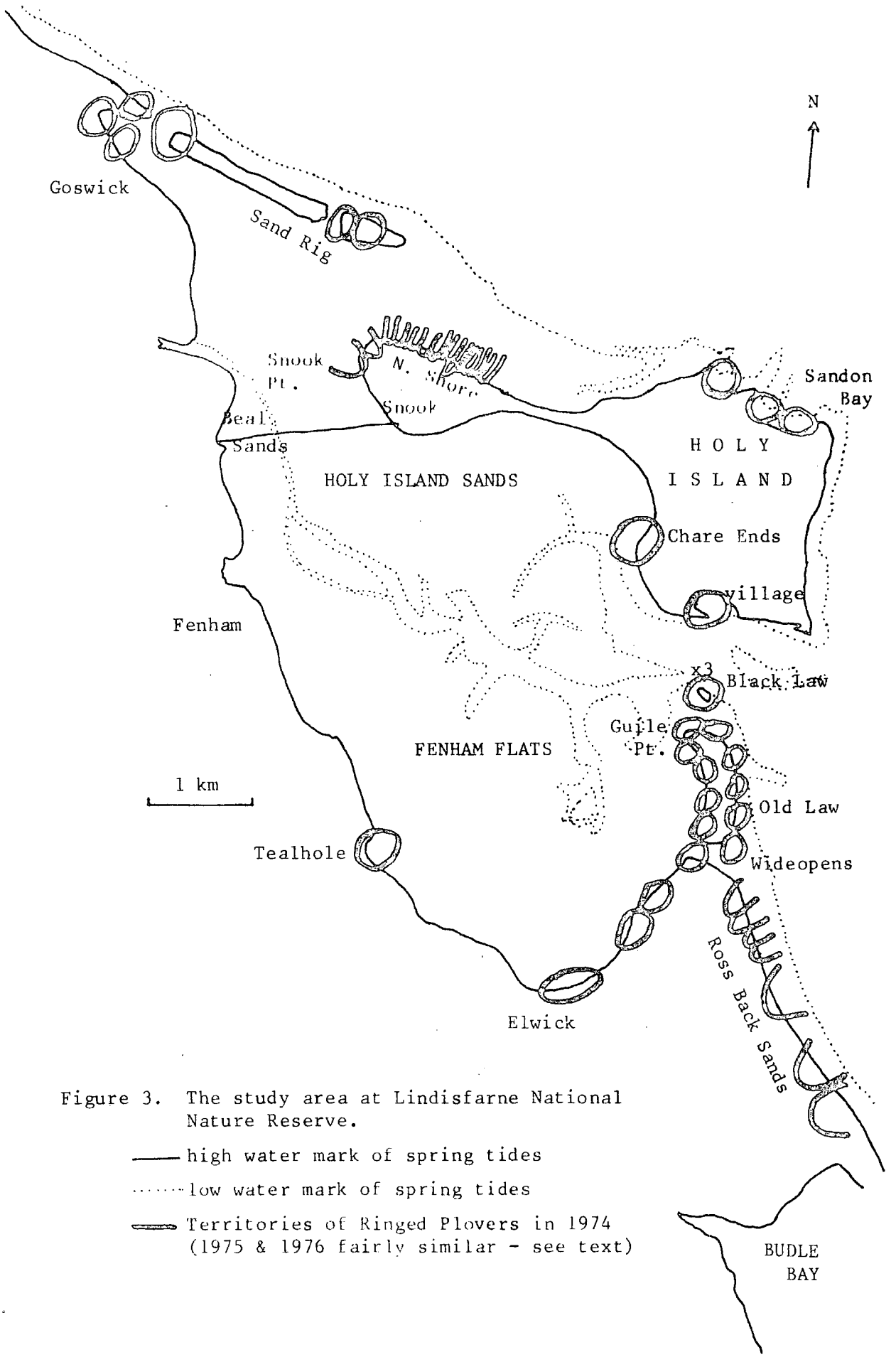


Figure 3. The study area at Lindisfarne National Nature Reserve.

——— high water mark of spring tides

····· low water mark of spring tides

═══ Territories of Ringed Plovers in 1974 (1975 & 1976 fairly similar - see text)

in 1974 (until mid-June), 1975 and 1976.

At Lindisfarne the Ringed Plovers nest on the shore and in sand dunes, gravel flats or occasionally on fields immediately adjacent to the shore. Most nests are close to intertidal areas, where much of the feeding takes place, although some birds nesting on sea beaches (e.g. Ross Back Sands) may move to the sheltered sand and mud-flats to feed.

METHODS

Bird distribution, territories and, where possible, feeding locations were mapped using observations of bird behaviour, made with a tripod-mounted 15-60 x telescope and 10x50 or 11x50 binoculars. Nests were found by searching suitable habitat in the territories or watching the birds' return from a concealed or distant viewpoint. The fates of nests were determined by regular checks and searches were made for indications of causes of loss in unsuccessful cases. It is possible that tracks and activities of observers and other persons in the area increased the predation rate on nests at Mestersvig (cf Willis 1973, Picozzi 1975). At Lindisfarne, it is unlikely that this had an effect, as observer activity formed only a small proportion of human activity in the area. To check on this, in 1976, a number of nests were inspected for much of the time only from a distance (by telescope) rather than by close approach. Predation on these nests did not differ from that on nests inspected closely.

Because of the difficulties in detecting nests on the date of laying of the first egg and the consequent over-estimation of survival rates, nesting success was calculated by Mayfield's (1961, 1975) 'exposure' method. This uses the field data to estimate the probability of a clutch being lost, by dividing the number of unsuccessful nests by the number of nest-days of observation. The estimated survival rate of a nest, from the laying of the first egg to hatching, is the daily chance of survival raised to the power d, where d is the number of days in this period. The method assumes that the chance of loss does not vary systematically through the laying and incubation period: checks on my data indicate this to be approximately true, apart from seasonal effects considered later. The only situations in

which observations were detailed enough to allow approximate estimates of nest survival from 1st egg to hatching by the 'conventional' method were at the North Shore in 1975 and 1976; 24% and 3% respectively (based on samples of nests of 29 and 30 respectively). These compare with 13% and 1% calculated by Mayfield's method. As expected, the 'conventional' estimates are higher because, even in the detailed study areas, some nests were not found until after the clutches had been lost (and others were probably not found at all). In other areas, because of less complete coverage and consequent biases in the conventional method, Mayfield's method is the only practicable one and this is used throughout this paper for data gathered in the present study and, where possible, from other sources.

The British Trust for Ornithology's Nest Record Cards for Ringed Plovers were also examined in an attempt to investigate egg production and nesting success in other sites. Unfortunately, serious difficulties in their use gradually became apparent. First, a large number of single-visit cards had to be ignored because they could not be used in estimating hatching success nor even clutch size. Second, many cards covered periods at unknown stages of incubation and their use, even for calculating mean clutch size, was dubious because of the uncertainty of previous losses of one or more eggs. Third, coverage through the breeding season is very uneven, often becoming non-existent at many sites later in the season. This is apparent from notes and dates of checks on some of the cards themselves and is reflected in the early end to the season indicated by these data (see Fig. 4). Fourth, and most serious, in a very large number of cases, the outcome of the nest was unknown, making estimates of survival rate by any method impossible. Disregard of such cases - which were typically a majority of cards for any region or year - could have introduced large and unknown biases. It is not clear how Prater (1974) dealt with such cards, as the method of analysis that he used, developed by D.I. Sales, has not yet been published. I investigated the possibility of restricting analysis to cards from certain sites, such as bird observatories and nature reserves, but it soon became clear that some biases applied here also. Thus, although nest record cards, as gathered by the current system, may be valuable for examining the breeding biology of, e.g. summer-visiting songbirds with a restricted breeding season and nidicolous young, their use for species

with a protracted season and, particularly, nidifugous chicks seems to be very limited. Instead of using the Nest Record Cards, therefore, some comparative information from other areas was obtained by correspondence with particular field workers who are acknowledged in the text.

Incubation schedules were monitored by watches at the nest from a hide placed nearby. In Greenland, these watches usually covered 24h periods, the hours 2400 to 0600 and 1200 to 1800 generally being covered by myself and 0600 to 1200 and 1800 to 2400 by another observer, generally D.I. North. Time of day is given as GMT (which is used locally, although solar midnight occurs at 0136). At this time of year the sun did not drop below the horizon, although it was lower in the sky (and in some situations was hidden by hills) around midnight so that 'nights' tended to be considerably cooler than 'days' (Paper 3). At Lindisfarne, only one observer was normally available and watches covered either the whole or most of the daylight period. Although at this latitude in summer the short nights are not very dark, it was not usually possible to see the incubating bird throughout the night. Some extra observations made by Miss S. Dick, Miss S. Jones, Miss S. Parkinson, F. Purnell and P. Snell, during undergraduate projects under my direction, are also utilised. Times were recorded as British Summer (or Standard) Time, solar midnight occurring at about 0108, so that times in the two areas are roughly comparable.

Attempts were made to locate feeding areas of nesting birds, to measure time spent feeding and feeding rates and to identify prey, as described in Papers 1 to 3. Seasonal fluctuations in 'terrestrial' (i.e. not inter-tidal) prey abundance were monitored by pitfall traps (Appendix 5 and Greenwood 1978).

During each observation period, note was kept of weather conditions, including air temperature at ground level, wind force and direction, and rainfall. In Greenland, these were supplemented by records at the meteorological station, which was within the study area. In both study areas, as many birds as possible were marked with combinations of colour rings unique to each individual.

RESULTS

Territorial establishment and egg-laying

Numerous Ringed Plovers were making stiff-winged ("butterfly") song flights over the areas clear of snow when the expedition arrived at Mestersvig on 25 June and these areas were the only ones where territories were established (Fig. 2). In other localities, notably

parts of the Nyhavn and Labben Hills, pairs established territories on snow-free patches of tundra but later deserted them, possibly when further snow clearance failed to reveal unvegetated areas, which Ringed Plovers always used for nesting. These pairs may later have established territories in more suitable areas but this seems unlikely, at least in the Mestersvig area; no territories were established late in the regularly censused area and it is unlikely that sufficient time for incubation and growth of young would remain for birds beginning to lay after early July. Many areas offering, after snow melt, apparently suitable nesting sites remained unutilised because snow clearance came too late (although some were used for rearing the young - see Paper 3). In some gravel areas, particularly in "Lemming Valley", fairly dense aggregations of pairs appeared to be trying to establish territories as the snow began to clear in late June and early July. By mid-July many of these defended areas were deserted: the remaining territories apparently enlarged to fill the space. The average size of 30 defended territories at Mestersvig was about 20 ha, although the pairs were generally widely spaced and disputes infrequent once territories had been established, so that boundaries were very diffuse.

During the period of territory establishment at Mestersvig birds appeared to feed both on the defended territory and in neutral areas. These undefended areas included a strip of marsh land and extensive melt water pools in the low ground beside the road between Mestersvig and Nyhavn. Such areas did not provide suitable nesting sites for Ringed Plovers and the birds did not attempt to defend them. The birds fed on both wet and dry areas but did not often wade in pools. As with other waders, the wet areas left by retreating snow cover was a favoured feeding habitat. Foraging was almost entirely by the typical plover "run-stop-peck" method, prey usually being taken from the surface of the vegetation and of the substrate; shallow probing was infrequent. Prey comprised a variety of invertebrates, particularly dipteran larvae and - as soon as they were available - adults, some larger larvae, and spiders (see Paper 3).

In all areas the birds nested on bare ground in shallow scrapes, unlined or sparsely lined with small stones, etc. At Mestersvig, egg laying followed soon after snow clearance and territory establishment (Figs. 4, 5). The laying dates of the first eggs of seven nests in

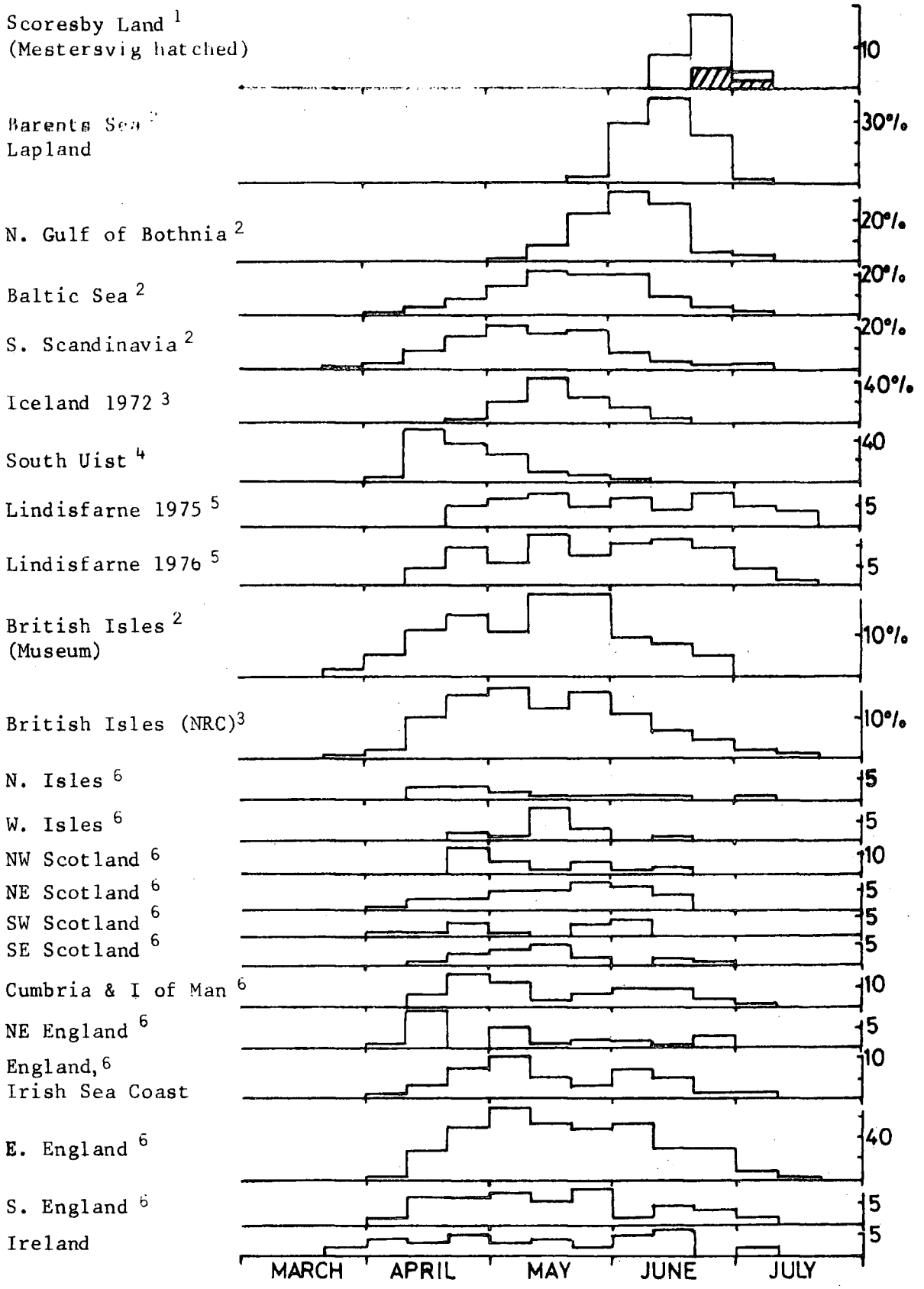


Figure 4. Distribution of dates of laying the first egg of Ringed Plover clutches in various areas.
Sources: [1]Green *et al.* (1977) & present study; [2]Väisänen (1977); [3]Prater (1974); [4]Wilson (1978); [5]Present study; [6]British Trust for Ornithology Nest Record Cards.

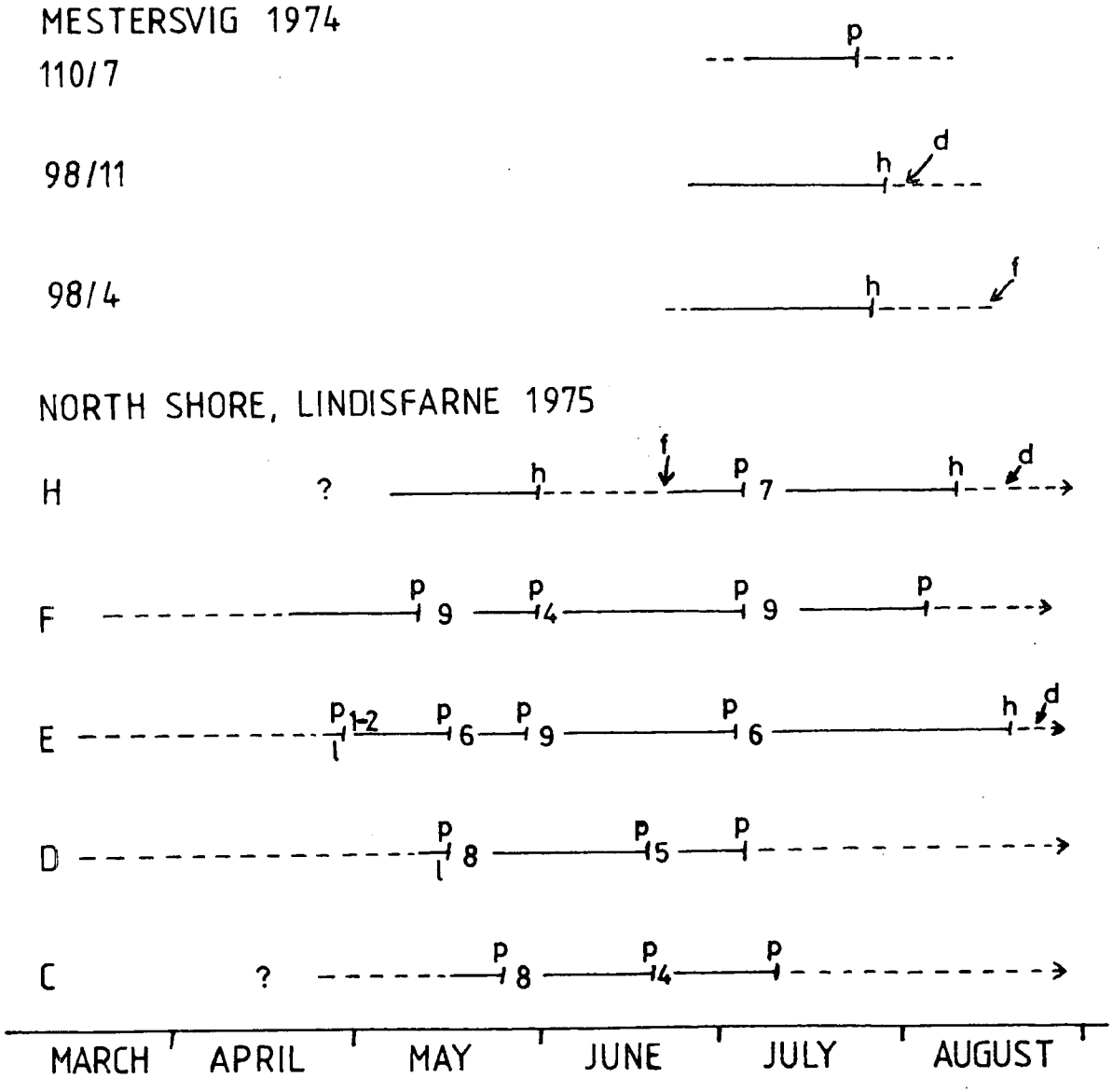


Figure 5. Example nesting histories.

---- birds on territory without nest

——— nest in existence

Numbers indicate days between loss and start of replacement clutches

P = eggs taken by predator

l = clutch not yet complete when lost

h = eggs hatch

d = chicks die

f = chicks fledge

the Mestersvig area were estimated to be between 22 June and 1 July, with both earlier and slightly later dates being recorded in other areas in Scoresby Land in the same year (Fig 4). Eggs were laid at approximately 1 day intervals, the clutch size at Mestersvig being 4 (11 cases) or 3 eggs (2) and in all areas in Scoresby Land 4(19) or 3(3), mean 3.86 (Green, Greenwood & Lloyd 1977, 1978; present study).

At Lindisfarne, territory establishment was a much more gradual process. Some birds stayed at Lindisfarne throughout the year, whereas others dispersed or migrated relatively short distances and returned from February onwards (Paper 3). Such birds typically joined the winter feeding flock on the intertidal flats and gradually spent increasing proportions of the day (both feeding and roosting) on territories from February onwards, most taking up permanent residence in March or April (Fig. 5).

Because birds nesting on the North Shore fed mainly on territory or to a lesser extent at nearby accessible communal feeding areas, it was possible to assess the amount of time spent feeding. For example, values for females on the North Shore on two days in late April before commencing nesting were 49% and 61% of the daylight hours spent feeding with probably virtually no feeding at night. Many casual observations also indicated that much of the available feeding time was not used and that the above values were fairly typical. Later in the season, during incubation, the maximum possible feeding time averaged, of course, 50% but non-incubating birds were seen to spend much of their time resting, preening, bathing, etc.

Territories were established around much of the shore of the Reserve (Fig. 3), the main exceptions being steep rocky shores or sites where mudflats and *Spartina* marshes reached the high water mark, leaving no gravel or sand area above the intertidal. Some areas, notably the North Shore of Holy Island Snook, Tealhole and the Guile Point area, seemed to hold territories of approximately constant size and position in each year. In these areas returning birds often took up the same territory as in previous years (Paper 3). In other areas, *viz.* parts of Goswick, the Sand Rig, Old Law and Ross Back Sands, the locations of territories varied more between years, possibly because

these beaches were more subject to changes in configuration by winter storms and by wind-blown sand at all times of year. These were also the areas where less feeding was generally done on territory (see below). Birds returning in successive years tended to return to the same general area, rather than to a particular territory (Paper 3). In extreme cases, e.g. part of the Elwick shore, over-winter changes in surface substrate appeared to make areas suitable for nesting in some years with high shores and some gravel expanses but unsuitable in others when shore level was lowered or gravel covered.

In all years at Lindisfarne, one or two pairs began to establish territories on the eastern end of the North Shore, but abandoned these without nesting by mid-May. This appeared to be associated with the increasing use of this shore (which is close to a car park and access point) by humans at this time of year.

Territory sizes at Lindisfarne varied greatly but were generally far smaller than in Greenland. On the North Shore, territories as small as about 0.3 ha were well defined (sometimes even by footprints left by opposing males walking parallel up and down the shore); whereas, at Ross and Goswick, more diffuse territories of over 10 ha were common. In the terneries at Black Law, in the Lindisfarne Reserve, and at Aberlady Bay, East Lothian, they were probably even smaller than on the North Shore. At Lindisfarne, territorial activity was maintained throughout the breeding season, presumably a result of the small, tightly packed territories and the frequently repeated nesting attempts (see below). Territory sizes previously reported for Ringed Plovers also range widely in different areas from about 0.06 ha in a closely packed group nesting in a tern colony in Co. Dublin (Mason 1947) to other large territories in Greenland (e.g. Meltofte 1979).

Laying dates of first eggs spread over several months (Fig. 4). The suggested bi- or tri- modality at Lindisfarne is known not to be due to renesting after a successful brood as there was only one case of this in each year. It arises instead from a certain degree of synchrony in the dates of predation of clutches, leading to some synchrony in laying of replacement clutches (see also below). Prater (1974) used the bimodality in the distribution of first-egg dates of

BTO Nest Record Cards as evidence for double brooding. Reanalysis of the Nest Record Cards (Fig. 4) indicates that the wide spread of first egg dates occurs throughout the British Isles (early dates are probably fairly reliable but the end of season data probably not - see Methods). As found by Prater (1974), there are some indications that the earliest start to the season occurs in Ireland, generally followed by Irish Sea coasts and much of England, with the latest in northern Scotland (but this may be due to lack of observer coverage before the tourist season there). At more northerly sites laying commences progressively later, as found by Vaisanen (1977) whose results are also summarized in Figure 4. First laying dates in Iceland and S. Scandinavia were somewhat later than the British Isles and considerably earlier than N. Scandinavia and Greenland. (The data for the end of the season in Iceland is incomplete because of a change in work-pattern of the observers there.) Laying dates on the Taimyr Peninsula (Krechmar 1966) appear to be fairly similar to those in NE Greenland.

Some information on laying intervals was obtained on the North Shore of Holy Island but this was limited because the frequency of nest visits was deliberately restricted to minimize the chance of attracting predators. Seventeen estimated intervals between egg-laying ranged from 1 to 3 days and averaged about 1½ days. Prater (1974) estimated slightly longer mean intervals of 1.74, 1.66 and 1.99 for the 3 inter-egg intervals respectively.

The mean clutch size (3.84, Table 1) was similar to the 3.86 found both in Greenland and in north Finland (Vaisainen 1969) and marginally higher than the 3.79 from British Nest Record Cards (Prater 1974) which may be biased by early losses of eggs and inclusion of incomplete clutches. One apparent case of a complete clutch of two eggs at Lindisfarne may possibly have been a case of very early loss of one or more eggs. One case of 5 eggs was observed but the laying frequency and birds responsible were not observed. The clutch was incubated for at least 40 days without hatching (the mean incubation period is 23.5 days - see below).

Incubation

Both sexes incubate, generally sharing the time fairly equally (Table 2), although there is some variation. Some of this may be an

TABLE 1. SIZES OF COMPLETE CLUTCHES OF RINGED PLOVERS AT LINDISFARNE

	No. of eggs/completed clutch				Mean clutch size
	2[a]	3[b]	4	5	
North Shore 1974		2	12		3.86
1975		5	22		3.81
1976	1	1	15		3.82
Ross Back Sands & Old Law 1976		5	23	1	3.86
All	1	13	72	1	3.84

Notes: [a]It is possible that this clutch had lost some eggs before discovery

[b]There was some tendency for 3-egg clutches to occur more as later replacement clutches

TABLE 2. SUMMARY OF SOME OBSERVATIONS OF INCUBATION SCHEDULES OF RINGED PLOVERS

Site	Date	Stage	Watch observation (h)	% of incubation time ♂	♀	none	Shift durations (mean) ♂	♀	Diurnal pattern
Mestersvig 1974									
Tunnelelv	2-3.7.74	early incubation	23.8	24	41	35	220,95,56,24,43 (89)	331+,200,20,95,30 (135+)	♀ aft-ev & early morn ♂ ev-night
S end runway*	5-6.7.74	early incubation	24.7	48	47	5	302,230,135 (222)	113+,190,128,275+ (177++)	♀ morning ♂ afternoon
N end runway	11-12.7.74	mid incubation	21.3	52	44	4	339+,80,13,17,96, 144+(115+)	85,21,167,64,181, 65+(97+)	♂ afternoon ♀ morning
Radio hut	17.7.74	mid incubation	24.0	60	38	2	666,215 (441)	151+,263,141+ (185++)	♂ mid aft-night ♀ night-mid aft
S end runway*	25.7.74	4 eggs chipping	35.7	31	49	20	38,155,56,80,61,40, 33,45,94,62,48(65)	142+,100,83,3,103, 370,128,28,124,29, 37,33+(98++)	no obvious pattern
S end runway* (*same nest)	28.7.74	hatching	12.1 (till 1st young leave nest)	33	60	7	81+,59,72,30(61+)	159,191,58,4(103)	no obvious pattern
Lindisfarne 1975									
Tealhole	22.5.75	early incubation	16.2	65	30	5	166,54,70,56,50,34, 224(93)	8,44,36,40,36,32, 95(41)	no obvious pattern
"	4.6.75	2nd week of incubation	16.1	55	44	1	96+,12,60,156,44, 36,36,28,64(59+)	44,36,56,24,32,68, 58,108(53)	no obvious pattern
North Shore (B)	1.6.75	early incubation	14.4	53	41	6	24,28,48,26,216, 36,48,44(59)	36,64,100,24,32,60, 56(53)	no obvious pattern
" "	9.6.75	mid incubation	11.2	38	62	0	36,104,118(86)	56,36,92,232+(104+)	slight tendency ♂ more morn ♀ more aft-ev
E Old Law	19.5.75	early incubation	11.9	47	46	7	44+,288(166+)	184,164(174)	no obvious pattern
North Shore (B)	1.6.75	early incubation	6.0	57	39	4	20+,20,20+,156+ (54++)	32,112(72)	slight tendency ♀ more morn ♂ more afternoon
North Shore (L)	1.6.75	early incubation	9.5	85	9	6	120+,336,32(163+)	36,16(26)	♂ more morn-aft
Snook end	6.6.75	early incubation	13.1	33	63	4	56,56,28,44,72+ (51+)	248,104,32,68,48 (100)	slight tendency ♀ more morn ♂ more afternoon
Elwick	14.6.75	early incubation	14.0	43	56	1	22,32,40,52,52,36, 28,16,24,36,24(33)	54,44,32,44,90,12, 68,32,16,44,28,12(40)	no diurnal pattern
North Shore (T/F)	19.6.75	10th day of incubation	11.9	41	56	3	14,32,36,225(77)	184,46,32,134(99)	v. slightly ♂ more morn & eve ♀ aft - i.e. little pattern

artifact of observations usually limited to 24h or less. Various authors (e.g. Walters 1957 for Kentish Plover *Charadrius alexandrinus*) have suggested that in some species there may be a regular diurnal pattern in the schedule of incubation of the two sexes. Although this appeared to be so for the Ringed Plover on some days, there seemed to be no consistent pattern within or between pairs and the suggested regularity at times may have resulted simply from the long incubation sessions in some sites (see below). There was no evidence that the female alone incubated at night, although the sex of the Lindisfarne birds could not be determined in darkness.

Incubation stints (i.e. the period between reliefs for which an individual was in attendence at the nest, including brief interruptions) were very variable in duration and no difference between the sexes was apparent. Variations with stage of incubation were difficult to assess, particularly at Lindisfarne, because of the high probability that any given nest under observation would not survive long, but little systematic change was apparent, possibly except a decrease in duration of each stint as activity increased around hatching time. Incubation stints tended to be longer in Greenland than at most of the Lindisfarne nests watched, except at the sea-beach at Old Law. On the basis of more casual observations, incidental to other activities such as catching, the longer stints are thought to be typical of this area and of Ross Back Sands. In common with the situation at Mestersvig, Ringed Plovers nesting on the sea-beaches of Old Law and Ross Back Sands generally move some distance to feed rather than doing so on territory and longer feeding periods are probably more efficient as distance to feeding grounds increases (cf Brown 1975, Brooke 1978).

During incubation at Mestersvig, apart from brief periods during change-over of incubating birds and during disturbance, most feeding took place well away from the nest. Colour-ringed birds were seen feeding over 3 km from their territory. This may have been a result of the rapid local variations in prey density and availability (see Greenwood 1974, 1978). Observed prey included various invertebrates, with spiders and adult Diptera most important. Adult and larval Lepidoptera were also observed as prey (Paper 3). As indicated above, at Lindisfarne the extent of feeding within the territory varied somewhat.

On the North Shore, most feeding took place on territory with some additional feeding, at times in flocks, on flats away from defended territories (Fig. 3). Birds from Ross Back Sands and the seaward beach of Old Law appeared to obtain most of their food on the intertidal flats on Budle Bay or west of Old Law away from the territory. Later in the season, however, family parties obtained most of their food in the area of the territory, at least initially, although some of the sea beach nesting birds later took their broods to the flats of Budle Bay or through Wideopens (Paper 3). Prey identified during observations on feeding is summarized in Appendix 1.

Generally the clutch was incubated for more than 90% of each day, but possibly less in the first days of incubation and at times just before hatching.

One incubation was abnormal in that the male took almost no part in it. This was the fifth nesting attempt by pair E on the North Shore in 1975, the first four having been unsuccessful (see Fig. 5). Up to and including the fourth nest, which was lost to predation at around the expected date of hatching at the end of June, both birds shared incubation normally. The male had started wing-moult by early July. (The starting of wing-moult by incubating birds in July is fairly common.) The birds displayed and made preliminary scrapes normally in the first few days of July, and the first egg of the fifth clutch was found on 9 July. By 13 July there were 3 eggs and incubation started, probably on that day. Observations during incubation are summarized in Table 3. The incubation period was abnormally long: 35 days to the hatching of the first young and the hatching was prolonged and asynchronous. The female was unable to both incubate eggs and brood young which had left the nest scrape. Detailed observations had to be stopped shortly after hatching and the young did not survive until the next check about a week later.

The percentage of time the eggs were incubated by this female alone (probably about 80%) is rather similar to that of some arctic wader species in which normally only one adult incubates, in contrast to the > 90% typical of 2-parent incubation, as are the frequent feeding excursions from the nest (Norton 1972, Pienkowski & Green 1976).

TABLE 3. INCUBATION AT NESTS OF TERRITORY E, NORTH SHORE, 1975

Date	Observation period	% time incubation by female*	% time no incubation	Duration (min) of incubation sessions: mean	s.d.(n)	Notes
13 July	1005 - 1556	74%	26%	22.3	16.3(12)	Male continues territorial behaviour and occasionally runs towards nest as if to incubate but stops short. Male has dropped first 2-3 inner primaries and replacements are well grown.
20 July	1040 - 2150	54%	41%	51.6	61.4(7)	Male behaves as above, additionally incubating once for 36 min. at most. Female off nest for one long period in afternoon as well as several shorter ones.
27 July	1049 - 2151	77%	23%	20.3	34.7(25)	Male still defends territory but does not show any signs of incubation or approaches to nest. Female leaves nest frequently to feed, chase intruders or to avoid people.
3 August	1012 - 1902	71%	29%	15.1	12.9(25)	Female has dropped first 1-2 inner feathers. Male still defending territory.
4 August to 17 August only female seen incubating during frequent checks						
12 August first egg 'stars'						
13 August all eggs starred						
14 - 17 August slow progress towards hatching by chicks						
17 August	1243 - 1813	78%	22%	18.4	15.1(14)	Male still present but showing little territorial activity and for a time associated with flock of non-breeding birds which spends some time nearby. 1 egg hatches late on 17 August.
18 August	Male still present but shows no interest in brooding chick even when this attempts brood with him. Female broods young but only occasionally spends brief times on nest. Second young hatches later that day; third not at all despite being well advanced in hatching.					

*These estimates are probably too low for the total proportion of the day spent incubating as the female spent more time off the nest feeding, etc. during the day than late in the evening, and presumably even less at night.

Single-adult incubation probably increases the conspicuousness of the nest to predators by virtue of the increased movements to and from the nest (see Pienkowski & Green 1976; *contra* Pitelka, Holmes & MacLean 1974). Clearly, in the Ringed Plover, neither the parents nor the eggs are adapted to single-adult incubation, which in this case resulted from the male's desertion presumably because of a change in hormonal condition towards the end of the breeding season. The female did not appear the following year and had presumably died in the interval. The male occupied the same territory in 1976.

One incubation period in Greenland was measured as 25-26 days. At Lindisfarne, four incubation periods were measured as 23 days and four as 24 days (mean 23.5) and the one exceptional case of 35 days (making the overall mean 24.8). The mean incubation period is similar to the 22-25 days reported by Bent (1929), 24 of Witherby *et al.* (1940) and 24.0 of Prater (1974). After allowing for the laying period and for the asynchrony of hatching, this gives a total period in the nest of about 29 days, and this figure is used below.

The birds left the nest to perform distraction displays if people and probably other ground predators approached. The reaction to potential aerial predators (notably Long-tailed Skuas *Stercorarius longicaudus*, Raven *Corvus corax* and Glaucous Gulls *Larus hyperboreus* at Mestersvig; Carrion Crows *Corvus corone*, Kestrels *Falco tinnunculus* and various gulls at Lindisfarne) varied. Usually the birds sat still, relying on camouflage, although occasionally the predators were mobbed, especially in higher-density nesting areas. Generally the reaction to predators, and the intensity and development of distraction displays, increased markedly just before the eggs hatched to a level typical of that of birds with young. The frequencies of disturbance from the nest by humans (which tended to be the most frequent cause observed) varied greatly between sites. At Mestersvig, the 6 hourly changes of observer and occasional movements by the observer were often the only human disturbances occurring. This was also true on some occasions at Old Law, Elwick and Tealhole, but on the Snook disturbance was much more intense especially at weekends and holidays when ten disturbances per hour during daylight were not uncommon.

Birds at both Mestersvig and Lindisfarne also occasionally left the nest to chase intruders, usually of the same species. Both sexes were involved in agonistic and anti-predator behaviour. There were some indications that males were more involved in agonistic exchanges when both birds were available to do this but this was more obvious both earlier, during territory establishment, and later, when with young.

Nesting success and failure and relayings

The nesting successes of Ringed Plovers in the present study and in other detailed studies are summarized in Table 4, which shows marked differences between sites and at the same site in different years. These differences are, in the main, statistically significant (e.g. Table 5). Further analyses (Tables 6-8) also demonstrate a seasonal difference in nesting success at Lindisfarne with early nests generally more likely to fail. Similar effects were also shown at some other sites.

Predators were the suspected cause of all nest losses at Mestersvig, Arctic Fox *Alopex lagopus* definitely being the agent in one case. Other potential predators were Stoat *Mustela erminea*, Long-tailed Skua, Glaucous Gull and Raven. One case of a Musk Ox *Ovibus moschatus* kicking an egg from a scrape and causing it to crack was suspected in one Greenland study area, and Musk Oxen did appear to be a potential danger to eggs at Mestersvig early in the season, as both species made use of the few areas clear of snow. Arctic Hares *Lepus arcticus* are suspected of damaging a clutch at Danmarkshavn (Meltofte 1979). As discussed in Paper 3, rates of predation on wader eggs and young at Mestersvig were probably higher than is typical for NE Greenland because of the higher density of predators around the station where they were sustained by scavenging from tips, etc. The values from Danmarkshavn and Baffinland (Table 4) may be more realistic, and Jehl (1971) also found higher hatching success (176 eggs hatched/219 eggs found - 80%) in Semipalmated Plovers at Churchill, Manitoba in 1964-67.

Causes of loss of whole clutches at Lindisfarne and St. Cyrus are summarized in Table 9. A few cases of flooding by spring tides (probably all those occurring being detected) were recorded in all situations; covering by blown sand may have been slightly more frequent than the identified cases indicate. A fairly wide range of predators were

TABLE 4. ESTIMATED PERCENTAGES OF NESTS SURVIVING TO HATCHING CALCULATED BY MAYFIELD'S METHOD, IN THE PRESENT AND OTHER DETAILED STUDIES

Location	Year	Nest-days	Losses	Survival/ nest day	Survival through laying and incubation
Mestersvig[1]	1974	182	6	0.9670	38%
Lindisfarne[1]	1975	393	25	0.9364	15%
including	Holy Island Snook	370	25	0.9324	13%
Lindisfarne[1]	1976	788	57	0.9277	11%
including	Ross Back Sands	212	11	0.9481	21%
	Old Law	311.5	9	0.9711	43%
	Holy Island Snook	250.5	35	0.8623	1.4%
Farne Islands, Northumberland[2]	1975	194	7	0.9639	34%
St. Cyrus, Fife[3]	1974	70.5	32	0.9585	29%
" " " [3]	1975	394	50	0.8731	2.0%
Uists, Outer Hebrides[4]	1973	374	10	0.9733	46%
		Clutches found	Clutches hatching		nest survival
Danmarkshavn, NE Greenland[5]	1975	9	7		78%
Home Bay, Baffin Island[6]	?	117	17		85%

Sources:

[1]Present study; [2]Messrs Heywood, Watts, Thompson & Chester (pers. comm. & Nest Record Cards); [3]N.K. Atkinson, *in litt.*; [4]J.R. Wilson, *in litt.*; [5]from Meltofte (1979). Although the Mayfield method cannot be used on the data available, nests were found during laying or early incubation and any over-estimation of survival is likely to be small; [6]from Smith (1969), by 'conventional' methods.

TABLE 5. COMPARISON OF NEST LOSSES BETWEEN AREAS OF LINDISFARNE NNR 1976

	Days without loss	Loss days	Total	Losses/ day
Ross & Old Law	503.5	20	523.5	0.04
Snook	215.5	35	250.5	0.14
All	719	55	774	0.07

$\chi^2 = 16.62$ $P < 0.001$

TABLE 6. ESTIMATED PERCENTAGES OF NESTS SURVIVING TO HATCHING IN RELATION TO AREA AND SEASON AT LINDISFARNE NNR

	Up to mid-May	Mid-May to mid-June	Mid-June onward	Total	No. of nest-days used	No. of nests used
			1975			
Snook	3.4%	40%	6.4%	13%	370	34
Total	3.4%	45%	6.4%	15%	393	35
			1976			
Ross Back Sands	3.6%	31%	31%	21%	212	15
Old Law	33%	20%	70%	43%	311.5	19
Snook	0.2%	2.4%	1.9%	1.4%	250.5	36
Others	-	0.2%	3.3%	1.1%	14	6
Total	2.8%	8.7%	22%	11%	788	76

TABLE 7. COMPARISON OF NEST LOSSES AT THE SNOOK, LINDISFARNE NNR, IN RELATION TO SEASON IN 1975

	Days without loss	Loss days	Total	Losses/day
Up to mid-May	47.5	6	53.5	0.11
Mid-May to mid June	179.5	5	184.5	0.03
Mid-June onwards	141	14	155	0.09
All	368	25	393	0.06

$\chi^2_2 = 18.51$ $P < 0.001$

TABLE 8. COMPARISON OF NEST LOSSES AT LINDISFARNE NNR IN RELATION TO SEASON IN 1976

	Days without losses	Loss days	Total	Losses/day
Up to mid-May	130	17	147	0.12
Mid-May to mid-June	227.5	20	247.5	0.08
Mid-June onwards	373.5	20	393.5	0.05
All	731	57	788	0.07

$\chi^2_2 = 7.17$ $P < 0.05$

TABLE 9. CAUSES OF LOSSES OF WHOLE CLUTCHES OF RINGED PLOVER EGGS AT LINDISFARNE NNR AND ST. CYRUS NNR

	Snook and Goswick		Ross Back Sands and Old Law		St. Cyrus[1]	
	1975	1976	1975	1976	1974	1975
Flooding by spring tide	2	1	1	2	1	2
Covering by blown sand			1			
Taken by:						
Dog	3	1			1	
Dog or Fox		3				
Fox	2	6	1	1		3
Rat *Rattus norvegicus*						2
Weasel *Mustela nivalis* or Rat		1				
Stoat					4	
Great Black-backed Gull *Larus marinus*					3	
Crow	1	5[4]		2	16	35
unknown predator	8	2			3	7
Man (taken or broken accidentally)		2	1		3	1
Disappearance: cause unknown	10	15	1	15		
Failure to hatch				1[3]		
Desertion	1[2]				1	1

[1]N.K. Atkinson (*in litt.*); [2]probably disturbed by man; [3]5-egg clutch (see text);
[4]including one taken by either Crow or Jackdaw *Corvus monedula*

responsible for most losses and there are signs that the causes of losses varied from place to place and year to year; note, for example, the difference between years at the Snook in the extent of predation by corvids. Observations of behaviour of Crows, of Fox *Vulpes vulpes* tracks, etc. suggest that relatively few individuals of both species may have been involved and that changes in their behaviour could have had marked effects on nest survival. During the period of most detailed coverage, 1976 at the Snook, nests were lost at the overall mean rate of 0.36 per day. However, non-loss days were significantly over-represented compared with the expected Poisson Distribution (Table 10). This was so, despite the numerous days when few (or only one)nests were available, making multiple losses impossible. There were indications of a similar pattern at St. Cyrus. As also pointed out with reference to nest losses of Golden Plovers *Pluvialis apricaria* (Ratcliffe 1976), predation may be of major importance to the numbers or breeding success of the prey but form only a small part of the predator's diet.

In one case at St. Cyrus and one at Lindisfarne (after the main study years) an adult bird was taken at the nest, probably by a fox and a dog respectively. Usually Ringed Plovers leave the nest to lure potential mammalian predators away while the latter are still distant, so that losses of adults at the nest are probably infrequent. However, an important element of Ringed Plover defence appears to be the unpredic tability of its behaviour (Meltofte 1976, 1977, 1979, Green 1978, present study) and sitting tight on the nest, more typical of some other wader species relying on camouflage, may be one extreme of this. This variable strategy may also be true of Golden Plovers (see Ratcliffe 1976).

At Mestersvig there were no partial losses of clutches and no cases of eggs failing to hatch. At Lindisfarne 6 of 121 (5%) eggs of successfully incubated clutches were lost before hatching. Prater (1974) obtained the same proportion from Nest Record Cards. In all cases at Lindisfarne, the eggs were thought to have been removed by humans; one such"predation" was witnessed and others probably deterred by the presence of observer or hide. Of the 115 eggs of successful clutches, 9 (8%) failed to hatch. These eggs included losses at various stages including some fully developed young where the failure

TABLE 10. COMPARISON OF NUMBERS OF RINGED PLOVER NESTS LOST PER DAY AT THE NORTH SHORE, LINDISFARNE NNR, IN 1976 WITH THE PATTERN OF LOSSES EXPECTED BY THE POISSON DISTRIBUTION IF LOSSES WERE INDEPENDENT

Losses per day	0	1	2	3	4	5	6
Observed frequency	82	15	5	1	1	0	1
Expected frequency	73.4	26.5			5.1		

Mean = 0.3619; $\chi^2_2 = 7.65$; $P < 0.05$

TABLE 11. NUMBERS OF NESTING ATTEMPTS ON THE NORTH SHORE PER PAIR PER SEASON

No. of attempts	1975[1]	1976[1]	Both years
0	1	1	2
1	1	0	1
2	7	1	8
3	3	4	7
4	0	4	4
5	1	0	1
mean	2.2	3.0	2.6

[1]Different sample sizes in the two years reflect different extents of detailed coverage.

The means for the two years do not differ significantly.

appeared to be due to an insufficient degree of synchrony between hatching times of eggs in the clutch. Prater (1974) estimated 6% from British Nest Record Cards and Meltofte (1979) found the same value at Danmrkshavn, Greenland. Some values for other species are 5% for Dotterel *Charadrius morinellus* (Pulliainen 1970), 4% for Golden Plover (Ratcliffe 1976), and 6% for Upland Sandpiper *Bartramia longicauda* (Higgins & Kirsch 1975).

At Mestersvig no unsuccessful nests were replaced probably because insufficient time for incubation and rearing remained. It is possible that there was sufficient time for replacement clutches in some other areas, such as Ørsted Dal and Karupelv (see Green, Greenwood & Lloyd 1977). At Danmarkshavn in 1975 several pairs probably renested after desertion during a late snow storm in mid-June around the time of laying (Meltofte 1979).

At Lindisfarne, the long season and high predation rate of chicks led to numerous renestings, the birds being able to relay, in a new scrape, within a few days of the loss (e.g. Fig. 5). Only two cases of "genuine" repeat (rather than "replacement") clutches were recorded, these being on the North Shore in 1975 and Old Law in 1976. The North Shore pair hatched their first brood (from a first clutch) on 1 June and relaid around the time these fledged and were still in the area of the territory in late June. This clutch was, however, lost in early July and replaced by a third in mid July. The young from this hatched on 8 August but did not survive until fledging. The Old Law pair hatched their first clutch on 28 May. The newly fledged young were still in the territory when the second full clutch was found on 27 June after the start of incubation. This hatched about 15 July and the young fledged in early August.

The numbers of nesting attempts in each year by each pair in the detailed study area are shown in Table 11. The higher mean number in 1976 reflects the higher loss rate in that year. No nest was found in one territory in both 1975 and 1976 (the same in both years) despite intensive searching and watching of the birds. Numerous 'display' and 'trial' scrapes were made and it seems possible that the birds were incapable of producing eggs. The birds concerned were not colour-

ringed, so it is not known if they were the same individuals in both years, although this seems likely.

DISCUSSION

Timing of breeding

Numerous studies have shown that in some species of birds the breeding season is timed either so that the young are being raised when food is most plentiful or so that eggs are laid as soon as sufficient food is available to the female to allow their production (e.g. Lack 1954, 1966, 1968, Perrins 1970, Källander 1974, Slagsvold 1975, Dunn 1976). Högstedt (1974) has presented evidence that this applies to at least one wader, the Lapwing *Vanellus vanellus* in southern Sweden, where the birds spend longer on territory before egg-laying if the density of available earthworms, their main prey, is low.

Many breeding waders, including Ringed Plovers, utilize the very high summer productivity of prey species, notably Diptera, in both arctic and temperate breeding grounds, to allow production and growth of their young (e.g. Holmes 1966a,b, Holmes & Pitelka 1968, Nettleship 1973, 1974, Paper 3). However, while an abundant available food source is clearly a prerequisite, changes in abundance do not necessarily determine the time of breeding. In the present study, in Greenland, the timing of snow clearance from nesting areas appeared to be the relevant factor, as evidenced by the observations at Mestersvig, the differences in date of nesting in other valleys with different timings of snow melt and the lack of a marked seasonal peak in prey availability. These results are discussed more fully by Green, Greenwood and Lloyd (1977) who also consider the differences between NE Greenland and some other high arctic areas.

At Lindisfarne, there is no such obvious determinant of the timing of breeding and the long delay between territory establishment and the commencement of laying is at first sight anomalous. Settled snow is fairly rare there even in mid-winter and nest sites are available throughout the season. It is unlikely that food for the laying female is critical, because both before and during incubation much potential feeding time is not utilised; available prey appears to be abundant throughout

the season (Paper 1 & Appendix 5); and the birds appeared to have no difficulty in obtaining most or all of their food from their small territories whereas Greenlandic birds foraged outside their larger territories. Also, throughout the season, egg production appeared not to be difficult, as relaying after the loss of a clutch commonly began within as little as 4 days (or, in the case on one nest lost to predation during laying, 1-2 days) and the replacement clutches apparently took no longer to produce (Fig. 5). Up to 5 clutches (mean 2.6) were produced by a female in a season (Table 11). Although there was a slight tendency for an increase in frequency of 3-egg clutches later in the season, the frequency remained low and there is no reason to suppose that a proximate factor (food shortage) was responsible. The reduced time taken to lay smaller clutches may have benefits later in the season when an earlier hatching of young by 1-2 days may be an appreciable benefit and the shortened nest exposure time reduces the risk of predation. (Many passerines lay smaller clutches later in the season, the principal reason for this put forward by Lack (1966) being the reduction in suitable food available for feeding the young later in the season. Such a cause is unlikely, however, for the case of Ringed Plovers, for reasons discussed in Paper 3.)

An alternative to the food-for-egg-formation argument is that by delaying laying, the birds are "insuring" against the risk of food shortage during incubation and a consequent need to desert (Brooke 1978). This seems unlikely to apply to Ringed Plovers because, apart from the reasons outlined above, desertion for any reason is rare (Table 9) and probably due to human interference when it does occur. Furthermore, nests of Ringed Plovers stand a high probability of loss for other reasons (Tables 3, 9). Also, incubation stints do not become shorter later in incubation (Table 3) as would be expected by Brooke (1978) if food was initially difficult (or time consuming or involved long journeys) to obtain but later became easier to collect.

Timing of production of young to coincide with prey abundance also seems a difficult hypothesis to apply to Ringed Plovers. Although there are indications of an increase in availability of flies in April and early May (Appendix 5), sandhoppers were already very numerous by then and intertidal prey were also available (Papers 1 & 2). Also,

the increase in fly abundance occurred well before the hatching of the first young, and if production of young is delayed to match increased fly availability, an earlier start would be expected because of the decreased probability of survival of young later in the season (Paper 3). Moreover, throughout the season the chicks appeared to have surplus feeding time, their rates of weight gain showed no sign of dependence on food availability and losses were due to other causes (Paper 3).

It also seems unlikely that the risk of severe weather early in the season delays nesting, as the conditions in the northern parts of the breeding range in June and July are considerably less clement than at Lindisfarne in April. The only conditions which caused prolonged brooding and cessation of feeding by the young was heavy rain on one day, fairly frequent low overnight temperatures in Greenland in August, and a single occasion of a freak snowfall on 1 June 1975 at Lindisfarne. Although severe weather has led to some desertions in Greenland (Meltofte 1974), the moderately cold, wet or windy weather in summer at Lindisfarne did not appear to depress hatching success. Indeed, one could argue that it had a beneficial effect, since tourists were deterred by it (see below).

The only feature that appears to account for the delay in commencement of nesting at Lindisfarne is the high risk of nest predation early in the season. This factor alone is probably sufficient to account for the late start to the breeding season as the probability of a clutch surviving to hatching before mid-May at Lindisfarne was only about 3% (Table 6).

The reason for the seasonal variation in incidence of predation is less clear and, as indicated above, generalizations on this aspect are particularly difficult because a large proportion of the losses may be due to the actions of a small number of individual predators to which eggs are a minor food source, so that small changes in the behaviour of these individuals may have marked effects on plover nesting success. Thus, the increase in alternative foods such as other birds' eggs and young Rabbits *Oryctolagus cuniculus* may decrease the predation pressure on Ringed Plover nests. Also, as the predators themselves breed, the spread of their activities may become more restricted. It

is also possible that Ringed Plovers may gain protection later in the season from other bird species nesting in the vicinity (notably terns which do not arrive till later), and this is explored later.

A breeding situation with some similarities to that of Ringed Plovers in both Greenland and Britain occurs in Golden Plover *Pluvialis apricaria* in S. Norway where, by observations and field experiments, Byrkjedal (1979; in press) found decreasing egg predation later in the season and attributed this to the high vulnerability of nests situated on small, snow-free, patches of ground.

Annual variability in hatching success may be common amongst waders, Purdue (1976b) reporting 29% to 100% in Snowy (= Kentish) Plover in the Great Salt Plains of Oklahoma, Harris (1967) 44% to 82% for Oystercatchers *Haematopus ostralegus* at Skokholm and Soikelli (1969, 1970) 30% to 97% for Dunlin *Calidris alpina* in Finland (note that some studies used different methods for calculating nesting success).

The end of the nesting season of Ringed Plovers may be determined by the need for adult birds to divert energy to other activities, such as moult at Lindisfarne or preparation for migration in Greenland, as evidenced by the incidence of a few desertions by one or other of the pair late in the season (and possibly by the failure to return next summer of a female left late in the season to incubate alone discussed earlier). The decreasing pre-fledging survival of chicks hatched late in the summer (Paper 3) may be a consequence of lack of adult attentiveness then, but may also have other causes which would lead the adults to reduce their investment in chick-rearing then.

Population dynamics

If a breeding population of animals is to be maintained without continual net immigration, the production of young surviving until reproductive age must not be exceeded by the mortality of the breeding adults.

The annual mortality of nesting adults (regardless of age) at Lindisfarne was 20% (Paper 3). (The same value is obtained by using weighted values of age-dependent mortality calculated in Paper 3.)

Thus each pair need to produce, on average, 0.4 surviving young per year. The figures relevant to production of young and their survival are summarised in Table 12. The observations suggest that at least some young birds are capable of breeding at one-year-old but only some do because of territoriality (Paper 3; Table 21), so the product of items 1 to 7 in Table 12 gives the mean number of potential recruits per pair per year: 2.24s at Lindisfarne. (Because of the number of components and their methods of calculation no confidence limits can be attached to this value.) For this value to exceed 0.4, $s > 0.4/2.24$, i.e. 0.179. It is clear from Table 4 that production of Ringed Plovers is marginally sufficient to replace losses in several study areas and totally inadequate in some years in some situations, notably Holy Island Snook in 1976 (and several years since then - Table 13 and unpublished data) and St. Cyrus in 1975.

Figures at Mestersvig are inadequate for the equivalent calculation to be made. However, using the Lindisfarne survival rates of adults and juveniles and the probable underestimates for chick survival, clutch survival of 0.36 is required for population stability. The acknowledged under-estimate of 0.38 exceeds this, and other, probably more typical, arctic estimates greatly so (Table 4).

Possible reasons for differences in breeding success between areas and years and their relevance to the geographical breeding distribution of the Ringed Plover

Apart from the erratic differences due to the behaviour of individual predators referred to above, several possible factors may give rise to the differences in Table 4. These include distribution of predators, conspicuousness and accessibility of nests to predation, intra- or inter-specific interference and protection, human interference and conservation measures.

The birds at the northern end of Old Law appeared to gain some warning of the approach of predators (or observers) from the adjacent ternery and the terns also appeared, incidentally to the defence of their own nests, to afford effective protection against aerial predators, which were mobbed. The observer at St. Cyrus (N.K. Atkinson *in litt.*) came independently to the same conclusion in accounting for the marked difference in nesting success in the two years there:

TABLE 12. SUMMARY OF DATA ON PRODUCTION AND SURVIVAL OF YOUNG RINGED PLOVERS

	Mestersvig	Lindisfarne	
1. Mean no. of clutches per pair per year	1	2.6	(Table 11)
2. Mean no. of eggs laid/clutch	3.86	3.84	(Table 1)
3. Probability of clutch surviving to hatching	s_m(0.38[1])	s	(see Tables 4 & 6)
4. Probability of eggs surviving in successful clutches	1	0.95	(text)
5. Probability of incubated egg in successful clutch hatching	1	0.92	(text)
6. Probability of hatched young fledging	0.5[1]	0.45	(Paper 3: Table 14)
7. Probability of fledged young surviving to 1 year old	n.d.	0.57	(Paper 3: Table 17)

[1]Probably atypically low for Scoresby Land

TABLE 13. SUMMARY OF RINGED PLOVER NESTING SUCCESS AT LINDISFARNE NNR IN 1977

Place	No. of clutches attempted	No. of clutches hatched	% success
North Shore	19	1	2%
Rest of Holy Island	16	5	31%
Ross Back Sands	15	5	33%
Old Law	31	18	58%
All other areas of NNR	8	1 ?	12.5% ?
Totals	89	30	34%

Source: P.A. Snell (*in litt.*)

"the main difference between 1974 and 1975 was the latter's late 'spring', which included gale-force NE winds in late May, snow showers on June 1st [see above] , and generally cold temperatures till mid-June. Apart from this, and possibly due to it, the Arctic Terns [*Sterna paradisaea*] (c. 65-70 pairs in 1974) did not really get going, and these definitely help the Ringed Plovers by keeping Crows out. Normally, the heaviest predation occurs from mid-April to late May, before the terns have started nesting, and later in July if they do not have a successful year."

The effect of tern protection from aerial predators is probably also relevant on the offshore Farne Islands (Northumberland) where the Ringed Plovers probably benefit also from the absence of ground predators and the control of human visitors by wardens. A similar effect occurs at Aberlady Bay, East Lothian, where nests in the ternery are more successful than those outside, although the situation is complicated by the exclusion of humans from the ternery (pers. obs.). There are several other anecdotal reports of Ringed Plovers benefitting from nesting in colonies of terns or Black-headed Gulls *Larus ridibundus*; on Scolt Head, Norfolk, nesting in a ternery afforded protection from Carrion Crows and Rooks *Corvus frugilegus* (Turner 1928). At this site also, some birds increased their chances of avoiding predation by nesting under branches of *Suaeda*. Similar behaviour was noted at Lindisfarne, where some birds on the North Shore occasionally nested under tree branches washed up on the shore, and some at Ross Back Sands commonly nested among marram grass. Walters (1957) reported that Kentish Plovers in the Netherlands often nest and find protection in colonies of Common Terns *Sterna hirundo* and Avocets *Recurvirostra avosetta*. Fuchs (1977) described a situation in Scotland where Sandwich Terns *Sterna sandvicensis* gained protection by breeding in colonies of other terns and Black-headed Gulls and apparently adjusted their time of breeding according to that of the 'protecting' species. There have been numerous other reports of various species gaining protection by nesting in such colonies (e.g. Bergman 1946, 1957, Ahlen & Andersson 1970, Bengtson 1972).

The effect of human disturbance may be the reason for the differences in nest survival in the three main areas at Lindisfarne (Table 4).

This difference was maintained in 1977 (Table 13) and probably in other years since (less systematic observations). The North Shore lies near the road to the tourist centre of Holy Island village and there are numerous access points to the beach and dunes. Access was unrestricted and generally unsupervised. Well over a hundred tourists were commonly recorded at the eastern end of the North Shore (east of the territories maintained through the summer, shown in Figure 3, but coinciding with the area where territories were abandoned early in the season). Many of these tourists walked around the Snook. At Ross Back Sands, where a walk of about 1.2 km is required from car park to nearest beach, rarely more than 40-50 people visited the area in a day; most stayed near the footpath access and only about a tenth walked around Old Law. Some direct deleterious effects of people were noted: 5 clutches of eggs were stepped on in 1977 (P.A. Snell, pers. comm.); single, or occasionally two, eggs were probably taken from clutches in each year (Table 9; and P.A. Snell, pers. comm.); dogs took several clutches (Table 9); and direct disturbance probably caused desertion of the eastern North Shore territories (see above; cf Hölzinger 1975). However, indirect effects of people and their dogs were probably more serious. Incubating birds normally left their nests when people or dogs approached, though a few birds developed considerable tolerance of people as the summer progressed. The more often the birds left the nests, the greater the opportunity for Carrion Crows to detect their movements to and from the nest. Some Crows appeared to use vantage points to watch for movements of disturbed birds. (Ringed Plovers often remain crouched on the nest and rely on camouflage in response to the presence of aerial predators, in contrast to their early departure at the approach of ground predators. At Lindisfarne most aerial predators are active in daylight and ground predators nocturnal but the presence of human potential 'ground predators' and the reaction to them potentially gives a considerable advantage to aerial predators.) In addition, increased bird movements to and from the nest led to more obvious trails of footprints in sandy areas and increased scent trails (possibly of the birds themselves but also well-meaning bird-watchers, and dogs) may have assisted foxes, weasels, etc. to locate clutches at night. A comparable interaction between human disturbance of incubating Black Oystercatchers *Haematopus moquini* in S. Africa and egg predation by gulls has been suggested by Summers & Cooper (1977), and

reported for Dunlins and gulls in Scotland (Hobson 1972).

The effect of mutual interference on nesting is difficult to assess. Various studies have argued that increasing density leads on the one hand to an increase in predation (Tinbergen 1952, Hinde 1956, Lack 1966, Tinbergen, Impekoven & Franck 1967) but on the other to increases in mutual alertness and protection within and between species (e.g. Hagen 1947, Kruuk 1964, Lack 1968, Kvaerne 1973, Goranssan *et al.* 1975, Slagvold 1980). Both such effects may apply to Ringed Plovers; predators appeared to use the proximity of nests on the North Shore to 'do the rounds' periodically but, conversely, adjacent pairs all performed distraction displays towards, or mobbed, potential predators (as also reported by Mason (1947) and Simmons 1956), undoubtedly causing confusion to them. No obvious pattern of predation rates in relation to density were apparent at Lindisfarne. Rates were highest at the North Shore and lowest at Old Law but both occurred in areas of high bird density and small territories. Intermediate predation rates were found at the larger, lower density Ross Back Sands territories.

The reason for the large variation in size of territories is unclear, partly because of the doubts which surround the function of territory in this species. Food supply for adults seems unlikely to be implicated because of the variation in the extent to which the territory is used for food gathering, at least before the young hatch. Safeguarding of food supply or a feeding area for family parties seems a more feasible function of a territory, but again this argument is weakened in that the territory may be deserted by the family, although this seems more frequent in larger and less productive territories: for example, it is more common at Ross Back Sands than North Shore and is typical in Greenland. Also compatible with the observed variation in nesting density is the suggestion that territories serve to space out nests according to the conspicuousness of nests in relation to nesting habitat. Thus, the highest densities occur at The Snook and Old Law where the substrate is gravel on which nests are best camouflaged; and lower densities are found on the sandy beaches of Goswick and Ross Back Sands where the nests are more obvious and are difficult to find mainly because of the expanse of sand or the marram cover. The lowest densities occur in Greenland where, at the time of laying and during the early part of incubation, the possible nest sites are

restricted to small clear areas, aiding searches by predators (cf Byrkjedal 1979 & in press). The present information cannot decide between these possibilities. Simmons (1956) argued that the main function of territory in the three small plovers is in spacing out of pairs and nests, but it is difficult to exclude totally the element of feeding of small young. Harris (1970) argued that territories were required for feeding young Oystercatchers at Skokholm but this wader species is exceptional in that the adults feed the young. Holmes (1970) argued that territory sizes of Dunlin in Alaska adjusted to allow enough food for adults early in the season but his paper does not adequately consider the effects of predation. For the same species in Finland, Soikkeli (1967) argued that the function of territory is to aid pair formation, but if this is the case, it is not clear why territory size should vary so markedly.

Variations in nest survival rate on a wide geographical scale may also be related to predation intensity and to the extent of available habitat in which to hide a nest. Generally, densities and number of species of potential predators, and the efficiency of predation due to increasing overall prey density, increase at lower latitudes (e.g. Larson 1960, Voous 1960, Connell 1971, Fretwell 1972, Dorst 1974, Maiorana 1976). The study of species diversity of waders in relation to latitude by Järvinen & Väisänen (1978) stressed the importance of increased habitat diversity in increasing species diversity, but commented that predation did not appear to be implicated in the increasing species diversity northwards. However, they appeared to consider increasing predation only as a factor which might reduce competition and thereby enhance species diversity, and not the reverse effect that increasing predation might limit the range of individual species and hence the number of species represented. Huffaker (1971) & Krebs (1972) cite numerous cases of predators affecting the distributions of prey species.

The extent of bare ground also decreases at lower latitudes, being restricted in W. Europe almost to the shoreline. The increasing predation and decrease in extent of bare ground would tend to increase the probability of nest predation and limit the southern extent of the breeding distribution. However, two closely related species breed further

south in Europe and North Africa than Ringed Plover. The Little Ringed Plover *Charadrius dubius* is an inland breeding species, typically found breeding on salt flats (Fig. 7). Its recent spread across Europe and its dependence on man-made, often transient, barren habitats such as gravel pits and newly reclaimed land, has been well documented (e.g. Parrinder 1964, Parslow 1967). The Kentish or Snowy Plover is largely a coastal species, like the Ringed Plover. It differs in being adapted to sand and clay, rather than gravel and stony, substrates by virtue of its body colouring, egg markings, egg covering behaviour (Meinertzhagen 1954, Simmons 1956, Hall 1960, Dybbro 1970, MacLean 1974) and nest concealment (Bent 1929, Rittinghaus 1961). It may also have particular adaptations to warmer conditions, such as egg cooling (Purdue 1976a, cf Begg & MacLean 1976), water shortage and high salinity (Purdue 1976b, Purdue & Haines 1977, cf MacLean 1976) and possibly different temperature tolerances for biochemical activity (see Chappell 1980).

There appears to be a latitudinal gradient in the distribution of gravel and sand on coasts (Fig. 6) and this seems to be matched closely by the breeding distributions of the two coastal species (Figs. 1, 7). Dybbro (1970) noted that, in Denmark near their northern limit, Kentish Plovers nested only in markedly sandy biotopes and that the breeding population had declined due to increased human activity in these areas. In the Netherlands where the three small plover species may breed alongside each other, they hold mutually exclusive territories and there may be some dominance relationship between species which could affect distribution (Sluiters 1954). The species may compete by the possible increase in nest predation with increasing density as, although all species will be affected, the probability of a nest being lost will be influenced by the match between egg camouflage and habitat (cf Fretwell 1972).

Southern limits of distribution and some implications for conservation

At the limits of a distribution, it is likely that breeding production will approximate to or be less than mortality. In the case of the Ringed Plover, there are indications that, in much of Britain, the species is only self supporting at sites where it receives some form of natural or artificial protection (Table 4): namely, off-shore

Figure 6. Predominant substrate types at top of depositing shores.

boulder, gravel, sand and gravel

sand, clay, mud

no data

Sources: Anon. (1947), INQUA (1967-75), Pienkowski (1975, pers. obs.) N.C. Davidson, P.J. Dugan & P.R. Evans (pers. comm.)

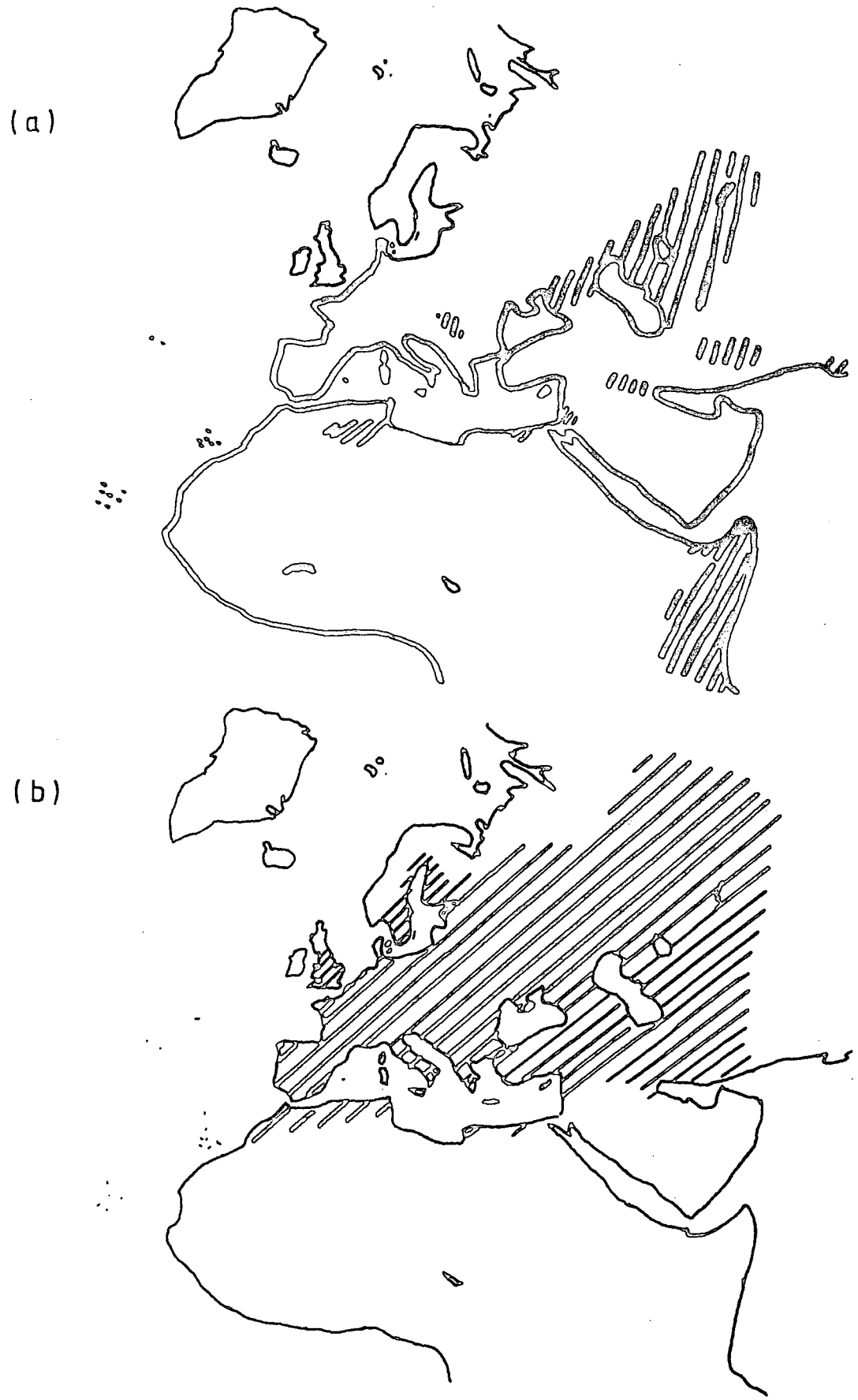


Figure 7. Distributions of (a) Kentish and (b) Little Ringed Plovers, according to Voous (1960). For Ringed Plover, see Figure 1.

islands protected from ground predators; tern colonies which provide defence against aerial predators; or nature reserves which can provide protection against some predators and/or people. These requirements may also apply to other species nesting in fairly open situations, and may be relevant to the southern limit of Turnstones *Arenaria interpres* on islands in the Baltic (Voous 1960, Larson 1960) and Long-tailed Duck *Clangula hyemalis* in the Arctic (Larson 1960). Colonial birds demonstrate this dependence on protected sites throughout much of their range, e.g. cliff- and island-nesting seabirds, but even in the Arctic, terns may have to wait until sea-ice melts before their nesting islands are safe from ground predators (Lack 1933, Bertram, Lack & Roberts 1934, Bird & Bird 1940, Larson 1960, Meltofte 1975). Many other species, including the waders Turnstone and Grey Phalarope *Phalaropus fulicarius*, appear to depend on island nesting sites for protection from predators in parts of their range (Larson 1960). The same author also argued that the breeding range of many arctic shorebirds and other species is limited by the intensity of predation by Arctic Fox, against which protective adaptations vary between species, so that the limits of prey distributions vary also.

For the Ringed Plover in W. Europe, usage of beaches by people and their dogs creates an additional adverse factor and this may be enough to change a positive net production to a negative one. If conservation of breeding populations of the species is required it may prove necessary to eliminate public access to certain areas and/or compensate for the effect of humans and dogs by reducing 'natural' predation - e.g. by reduction or exclusion of some predators (e.g. Forster 1975). A comparable situation appears to exist in breeding Black Oystercatchers in S. Africa (Summers & Cooper 1977).

An added complication is the interaction of possible effects on breeding success (Fig. 8) so that the situation if public access were to be restricted cannot be predicted. This may apply to the detailed study area at the North Shore. Public access to the area has increased markedly in recent years, both because of increased leisure, wealth and car-ownership of the population (e.g. Speight 1973; pers. comm. from local residents) and the progressive building of a road to the island, completed in the 1960's. These have probably had direct effects

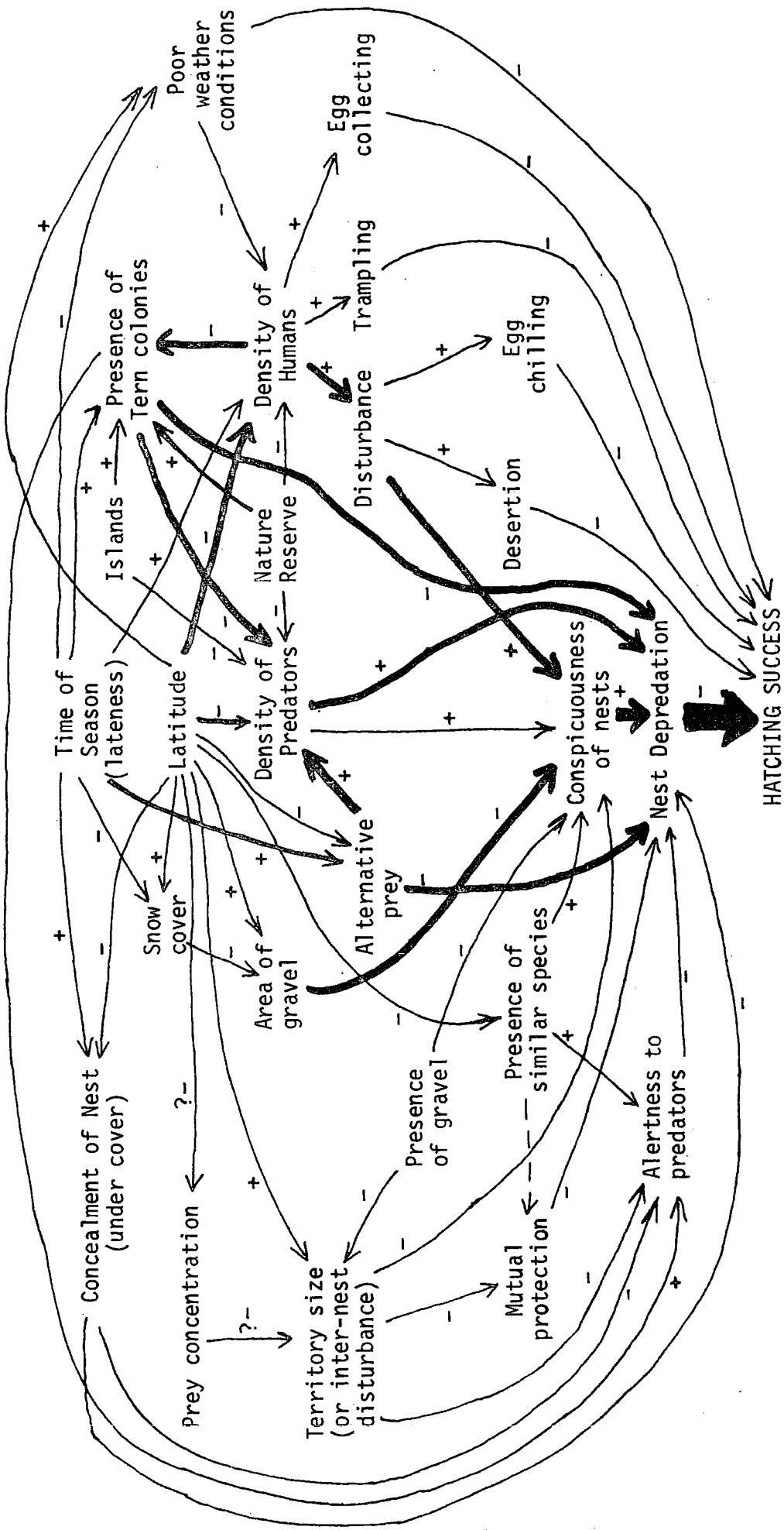


Figure 8. Likely interactions between some factors affecting nesting success of Ringed Plovers. Thickness of lines gives very approximate indication of relative importance. (Egg camouflage, bird camouflage, anti-predator behaviour, etc. not shown).

on the Ringed Plovers but also via the terns as the former North shore ternery has disappeared (pers. comm. from Holy Islanders). (It has disappeared, probably due to human disturbance (Bolam 1912), and reappeared at least once in the past.) Also, management policy has changed; in former years the local fox-hunt was allowed to visit the island but this stopped some time after the establishment of the Nature Reserve in 1964; and changes have also occurred in keepering on local estates. There have also been what appear to be natural topographical changes, for example in the route of the channel along the North Shore, giving rise to a much narrower beach here than that shown by Perry (1945).

Against such a background, it is difficult to know how much the behaviour of Ringed Plovers and their apparent preference for the North Shore is fitted to the present situation and how much is an historical effect, especially when the fairly high adult survival (and consequent delay before a decline in production might become apparent) are taken into account. Indeed, the situation may not be stable at all: will the low production and poor success in this area eventually lead to its abandonment despite it having had the highest density of breeding Ringed Plovers recorded during the study? Since the birds show some flexibility in behaviour, such as nesting under cover and in fields, pairs might move to other habitats. The tendency to nest farther from the shore might increase as has apparently happened in Oystercatchers (Heppleston 1972; see also Prater 1976). On the other hand, high densities on the shore have a long history and high nest predation rates have long been suffered at Lindisfarne. Bolam (1912) noted that, at Ross Links and Holy Island, " on the shore, just above high water mark, and in stony depressions amongst the sandhills . . . I have sometimes seen three or four nests, all containing eggs, within ten or twenty yards of one another." Unfortunately the extent of nest predation was not quantified but was sufficient for Bolam to remark on the birds "patiently laying again as often as its eggs were taken (as they used to be on a wholesale manner until a few years ago), and persisting in doing so until happy chance enabled it to bring off a brood, or the advanced season had satiated the Islanders' proclivities for birds'-nesting." The protecting effect of other birds was also noted: "On the Farne Islands, the Ringed Plover also breeds on the

outskirts of the clamorous colonies of Terns, appreciating, perhaps, the protection which the latter afford in keeping off marauding Gulls." A few terns, mainly Arctic, nested at several sites on the seaward side of the reserve, including the Snook at this time, although subject to egg collecting (see Bolam 1912). Hence, it is difficult to decide if low nesting success of Ringed Plovers in parts of the Lindisfarne Reserve is a new situation or of long standing. The various possible causes of low success could be investigated further only by field experiments, such as the restriction of access to humans or various predators.

SUMMARY

The nesting of Ringed Plovers was investigated in 1974 at Mestersvig, NE Greenland, and in 1974-76 at Lindisfarne, NE England. Difficulties in the use of Nest Record Cards for this species are discussed.

Territory establishment, distribution and sizes, the timing of egg laying and clutch sizes in different areas are compared. Incubation (mean period about 25 days) was shared fairly equally by the two sexes and variations in the incubation schedule appeared to be related to local geography. Nesting success varied greatly in different areas and years and in relation to timing within a season. Most egg losses were probably due to predation. Up to five nestings per pair per year were made at Lindisfarne where nest losses were very high.

The timing of breeding is discussed and it is concluded that the date of start of egg-laying in NE Greenland is determined by the timing of snow clearance while that at Lindisfarne is related to the decreasing probability of egg-predation later in the season. Because of the high nest losses, the production of young at many temperate sites, including parts of Lindisfarne, was probably inadequate for the population to be self-supporting, and the reasons for the large seasonal, annual and geographical differences are discussed. It is concluded that increasing predation probably determines the southern nesting limits of Ringed Plovers but that this limit may be modified by varying degrees of different types of natural and artificial protection. Increased human usage of nesting beaches probably has an adverse effect on nesting success but, because of the complexity of the number of inter-related factors affecting the latter, without field experiments it is difficult to predict how this could best be offset by protection measures.

REFERENCES

Ahlén, I. & Andersson, Å. 1970. Breeding ecology of an eider population on Spitzbergen. *Ornis Scand.* 1: 83-106

Anonymous, 1947. Admiralty surveys of west and north west African coasts

Begg, G.W. & Maclean, G.L. 1976. Belly soaking in the Whitecrowned Plover. *Ostrich* 46: 65

Bengtson, S.-A. 1972. Reproduction and fluctuations in the size of duck populations at Lake Myvatn, Iceland. *Oikos* 23: 35-58

Bent, A.C. 1929. Life histories of North American shorebirds. Part II. *U.S. Nat.Mus.Bull.* 146

Bergmann, G. 1946. Der Steinwälzer, *Arenaria i. interpres* (L.), in seiner Beziehung zur Umwelt. *Acta Zool.Fenn.* 47: 1-151

Bergmann, G. 1957. Zum Problem der gemischten Kolonien: Die Reiherente (*Aythya fuligula*) und die Lariden. *Vogelwarte* 19: 15-25

Bertram, G.C.L., Lack, D. & Roberts, B.B. 1934. Notes on East Greenland birds, with a discussion of the periodic non-breeding among arctic birds. *Ibis* (13)14: 816-831

Bird, C.G. & Bird, E.G. 1940. Some remarks on non-breeding in the Arctic, especially in north-east Greenland. *Ibis* (14)4: 671-678

Bolam, G. 1912. *The Birds of Northumberland and the Eastern Borders.* Henry Hunter Blair, Alnwick

Brooke, M. de L. 1978. Some factors affecting the laying date, incubation and breeding success of the manx shearwater, *Puffinus puffinus*. *J.Anim.Ecol.* 47: 477-495

Brown, W.Y. 1975. Incubation shifts of Sooty Terns *Sterna fuscata* on Manana Island, Hawaii. *Ibis* 117: 527-529

Byrkjedal, I. 1979. Nest predation in relation to snow-cover as a factor influencing the start of breeding in shorebirds (abstract). *Wader Study Group Bull.* 26: 23

Byrkjedal, I. in press. Nest predation in relation to snow-cover as a factor influencing the start of breeding in shorebirds. *Ornis Scand.*

Chappell, M.A. 1980. Thermal energetics of chicks of arctic-breeding shorebirds. *Comp.Biochem.Physiol.* 65A: 311-317

Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. pp 298-312 in P.J. den Boer & G.R. Gradwell (eds.) *Dynamics of Populations: Proceedings of the Advanced Study Institue on 'Dynamics of Numbers in Populations', Oosterbeek, the Netherlands, 7-18 September 1970.* Centre for Agricultural Publishing and Documentation, Wageningen

Dorst, J. 1974. *The Life of Birds*. 2 vols. Weidenfeld & Nicolson, London

Dunn, E.K. 1976. Laying dates of four species of tits in Wytham Wood, Oxfordshire. *Brit. Birds* 69: 45-50

Dybbro, T. 1970. The Kentish Plover (*Charadrius alexandrinus*) as a breeding bird in Denmark. *Dansk orn.Foren.Tidsskr.* 64: 205-222 (in Danish with English summary)

Edwards, G., Hosking, E. & Smith, S. 1947. Aggressive display of the Ringed Plover. *Brit. Birds* 40: 12-19

Ferns, P.N. 1978. Ecological distribution of wading birds. pp 79-84 in Green & Greenwood (1978)

Forster, J.A. 1975. Electric fence to protect sandwich terns against foxes. *Biol. Conserv.* 7: 85

Fretwell, S.D. 1972. *Populations in a Seasonal Environment*. Princeton Univ. Press, Princeton

Fuchs, E. 1977. Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. *Ornis Scand.* 8: 17-31

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. 1975. *Handbuch der Vögel Mitteleuropas*. Band 6. Akademische Verlagsgesellschaft, Wiesbaden

Göransson, G., Karlsson, J., Nilsson, S.G. & Ulfstrand, S. 1975. Predation on birds' nests in relation to anti-predator aggression and nest density: an experimental study. *Oikos* 26: 117-120

Green, G.H. 1978. The census of waders. pp 84-109 in Green & Greenwood (1978)

Green, G.H. & Greenwood, J.J.D. (Eds.) 1978. *Joint Biological Expedition to North East Greenland 1974*: the report of the joint expedition comprising Wader Study Group NE Greenland Expedition 1974 and Dundee University NE Greenland Expedition 1974. Dundee University NE Greenland Expedition, Dundee

Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. *J.Zool.,Lond.* 183: 311-328

Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1978. The effect of snow conditions on the date of breeding in waders. pp 75-78 in Green & Greenwood (1978)

Green, G.H., Pienkowski, M.W., Brown, S.C., Ferns, P.N. & Mudge, G.P. 1978. Methods used for wader studies. pp 38-51 in Green & Greenwood (1978)

Greenwood, J.J.D. 1974. The distribution and activity of tundra arthropods. pp 48-55 in O'Brien & Greenwood (Eds.) *Report of the University of Dundee N.E. Greenland Expedition 1972.* Dundee University N.E. Greenland Expedition, Dundee

Greenwood, J.J.D. 1978. Activity patterns and habitat distribution of tundra invertebrates. pp 168-182 in Green & Greenwood (1978)

Hagen, Y. 1947. Spiller dvergfalken i enkelte tilfeller en rolle som beskytter av gråtrostkolonier i fjellet ? *Vår Fagelvärld* 6: 137-141

Hall, K.R.L. 1960. Egg-covering by the White-fronted Sandplover. *Ibis* 102: 545-553

Harris, M.P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. *Ibis* 109: 180-193

Harris, M.P. 1970. Territory limiting the size of the breeding population of the Oystercatcher (*Haematopus ostralegus*) - a removal experiment. *J.Anim.Ecol.* 39: 707-713

Heppleston, P.B. 1972. The comparative breeding ecology of oystercatchers (*Haematopus ostralegus* L.) on inland and coastal habitats. *J.Anim.Ecol.* 41: 23-51

Higgins, K.F. & Kirsch, L.M. 1975. Some aspects of the breeding biology of the Upland Sandpiper in North Dakota. *Wilson Bull.* 87: 96-102

Hinde, R.A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-389

Hobson, W. 1972. Breeding biology of the Knot. *Proc. Western Foundation of Vert. Zool.* 2: 5-25

Högstedt, G. 1974. Length of the pre-laying period in the Lapwing *Vanellus vanellus* L. in relation to its food resources. *Ornis Scand.* 5: 1-4

Holmes, R.T. 1966a. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. *Condor* 68: 3-46

Holmes, R.T. 1966b. Feeding ecology of the Red-backed Sandpiper (*Calidris alpina*) in arctic Alaska. *Ecology* 47: 32-45

Holmes, R.T. 1970. Differences in population density, territoriality, and food supply of Dunlin on arctic and subarctic tundra. pp 303-319 in A. Watson (ed.) *Animal Populations in Relation to their Food Resources.* Blackwell, Oxford & Edinburgh

Holmes, R.T. & Pitelka, F.A. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. *Syst.Zool.* 17: 305-318

Hölzinger, J. 1975. Untersuchungen zum Verhalten des Flussregenpfeifers *Charadrius dubius* bei gestortem und ungestortem Brutablauf. *Ans.orn.Ges.Bayern* 14: 166-173

Huffaker, C.B. 1971. The phenomenon of predation and its roles in nature. pp 327-343 in P.J. den Boer & G.R. Gradwell (eds.) *Dynamics of Populations. Proceedings of the Advanced Study Institute on 'Dynamics of Numbers of Populations', Oosterbeck, the Netherlands, 7-18 September 1970.* Centre for Agricultural Publishing and Documentation, Wageningen

INQUA, 1967-75. *International Quaternary Map of Europe.* Sheets 1-8, 11, 12. Bundesanstalt für Bodenfaorschung, Hanover and UNESCO, Paris

Järvinen, O. & Väisänen, R.A. 1978. Ecological zoogeography of North European waders, or Why do so many waders breed in the North? *Oikos* 30: 495-507

Jehl, J.R. 1971. Patterns of hatching success in subarctic birds. *Ecology* 52: 169-175

Källander, R. 1974. Advancement of laying of Great Tits by the provision of food. *Ibis* 116: 365-367

Krebs, C.J. 1972. *Ecology. The experimental analysis of distribution and abundance.* Harper & Row, New York

Krechmar, A.V. 1966. The birds of the western parts of the Taimyr Peninsula. *Trudy zool.Inst.Leningrad* 30: 185-312 (in Russian)

Kruuk, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). *Behaviour Suppl.* 11: 1-120

Kvaerne, M. 1973. Kan vipa vaere vaktfugl for andre fuglearter ? *Sterna* 12: 85-90

Lack, D. 1933. Nesting conditions as a factor controlling breeding time in birds. *Proc. Zool.Soc.Lond.* 1933: 305-318

Lack, D. 1954. *The Natural Regulation of Animal Numbers.* Clarendon Press, Oxford

Lack, D. 1966. *Population Studies of Birds.* Clarendon Press, Oxford

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds.* Methuen, London

Larson, S. 1960. On the influence of the Arctic Fox *Alopex lagopus* on the distribution of arctic birds. *Oikos* 11: 276-305

Laven, H. 1940. Beiträge zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.) *J.Orn.* 88: 183-281

Maclean, G.L. 1974. Egg-covering in the Charadrii. *Ostrich* 45: 167-174

Maclean, G.L. 1976. A field study of the Australian Pratincole. *Emu* 76: 171-182

Maiorana, V.C. 1976. Predation, submergent behaviour, and tropical diversity. *Evol. Theory* 1: 157-177

Mason, A.G. 1947. Territory in the Ringed Plover. *Brit. Birds* 40: 66-70

Mayfield, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255-261

Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456-466

Meinertzhagen, R. 1954. *Birds of Arabia.* Oliver & Boyd, Edinburgh

Meltofte, H. 1975. Ornithological observations in northeast Greenland between 76°00' and 78°00'N Lat. 1969-71. *Medd. om Grønland* 191(9): 1-72

Meltofte, H. 1976. Ornithological observations in southern Peary Land, north Greenland, 1973. *Medd. om Grønland* 205(1): 1-57

Meltofte, H. 1977. 'Fly-away trick' of some arctic waders. *Brit. Birds* 70: 333-336

Meltofte, H. 1979. The population of waders Charadriidae at Danmarks Havn, Northeast Greenland, 1975. *Dansk orn.Foren. Tidsskr.* 73: 69-94

Nettleship, D.N. 1973. Breeding ecology of Turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. *Ibis* 115: 202-217

Nettleship, D.N. 1974. The breeding of the Knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N.W.T. *Polarforchung* 44: 8-26

Norton, D.W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. *Condor* 74: 164-176

Parrinder, E.R. 1964. Little Ringed Plovers in Britain during 1960-62. *Brit. Birds* 57: 191-198

Parslow, J.L.F. 1967. Changes in status among breeding birds in Britain and Ireland. *Brit. Birds* 60: 97-123

Perry, R. 1945. *A Naturalist on Lindisfarne.* Lindsay Drummond, London

Perrins, C.M. 1970. The timing of birds' breeding seasons. *Ibis* 112: 242-255

Picozzi, N. 1975. Crow predation on marked nests. *J.Wildlife Management* 39: 151-155

Pienkowski, M.W. 1980. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Proc. IWRB Feeding Ecology Symp., Gwatt, Switzerland, September 1977. *Verh.Orn.Ges. Bayern* 23: (in press)

Pienkowski, M.W. (Ed.) 1975. *Studies on coastal birds and wetlands in Morocco 1972.* Joint report of University of East Anglia Expedition to Tarfaya Province, Morocco 1972 and Cambridge Sidi Moussa Expedition 1972. Norwich

Pienkowski, M.W. & Green, G.H. 1976. Breeding biology of Sanderlings in north-east Greenland. *Brit. Birds* 69: 165-177

Pitelka, F.A., Holmes, R.T. & MacLean, S.F. 1974. Ecology and evolution of social organization in arctic sandpipers. *Amer. Zool.* 14: 185-204

Prater, A.J. 1974. Breeding biology of the Ringed Plover *Charadrius hiaticula*. *Proc. IWRB Wader Symp. Warsaw 1973*: 15-22

Prater, A.J. 1976. Breeding population of the Ringed Plover in Britain. *Bird Study* 23: 155-161

Pulliainen, E. 1970. On the breeding biology of the Dotterel *Charadrius morinellus*. *Ornis Fenn.* 47: 69-73

Purdue, J.R. 1976a. Thermal environment of the nest and related parental behaviour in Snowy Plovers *Charadrius alexandrinus*. *Condor* 78: 180-185

Purdue, J.R. 1976b. Adaptations of the Snowy Plover on the Great Salt Plains, Oklahoma. *Southwestern Naturalist* 21: 347-357

Purdue, J.R. & Haines, H. 1977. Salt water tolerance and water turnover in the Snowy Plover. *Auk* 94: 248-255

Ratcliffe, D.A. 1976. Observations on the breeding of the Golden Plover in Great Britain. *Bird Study* 23: 63-116

Rittinghaus, H. 1956. Untersuchungen am Seeregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeoog. *J.Orn.* 97: 117-155

Rittinghaus, H. 1961. *Der Seeregenpfeifer*. A. Ziemsen Verlag, Wittenberg, Lutherstadt

Salomonsen, F. 1950. *The Birds of Greenland*. Munksgaard, Copenhagen

Simmons, K.E.L. 1953. Some aspects of the aggressive behaviour of three closely related plovers (*Charadrius*). *Ibis* 95: 115-127

Simmons, K.E.L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape- and brooding drives. *Behaviour* 8: 130-173

Simmons, K.E.L. 1956. Territory in the Little Ringed Plover *Charadrius dubius*. *Ibis* 98: 390-397

Slagsvold, T. 1975. Breeding time of birds in relation to latitude. *Norw. J. Zool.* 23: 213-218

Slagsvold, T. 1980. Egg predation in woodland in relation to the presence and density of breeding Fieldfares *Turdus pilaris*. *Ornis Scand.* 11: 92-98

Sluiters, J.E. 1954. Observations on the Kentish, Little Ringed and Ringed Plover, breeding near Amsterdam. *Limosa* 27: 71-86 (in Dutch with English summary).

Smith, N.G. 1969. Polymorphism in Ringed Plovers. *Ibis* 111: 175-188

Soikkeli, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). *Ann.Zool.Fenn.* 4: 158-198

Soikkeli, M. 1970. Mortality and reproductive rates in a Finnish population of Dunlin *Calidris alpina*. *Ornis Fenn.* 47: 149-158

Speight, M.C.D. 1973. Outdoor recreation and its ecological effects. *University College London Discussion Papers in Conservation* No. 4, 35 pp

Summers, R.W. & Cooper, J. 1977. The population, ecology and conservation of the Black Oystercatcher *Haematopus moquini*. *Ostrich* 48: 28-40

Sutton, G.M. & Parmelee, D.F. 1955. Breeding of the Semipalmated Plover on Baffin Island. *Bird-Banding* 26: 137-147

Tinbergen, N. 1952. On the significance of territory in the Herring Gull. *Ibis* 94: 158-159

Tinbergen, N., Impekoven, M. & Franck, D. 1967. An experiment on spacing-out as a defence against predation. *Behaviour* 28: 307-321

Turner, E.L. 1928. *Bird Watching on Scolt Head*. Country Life, London

Väisänen, R.A. 1969. Evolution of the Ringed Plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. A new computer method based on egg dimensions. *Ann.Acad.Sci. Fenn.* AIV, 149: 1-90

Väisänen, R.A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. *Ann.Zool. Fenn.* 14: 1-25

Voous, K.H. 1960. *Atlas of European Birds*. Nelson, London

Walters, J. 1957. Behaviour during the egg-laying period in the Kentish Plover (*Charadrius alexandrinus* L.), and the division of labour during the nesting cycle. *Ardea* 45: 24-62 (in Dutch with English summary)

Willis, E.O. 1973. Survival rates for visited and unvisited nests of Bicolored Antbirds. *Auk* 90: 263-267

Wilson, J.R. 1978. Agricultural influences on waders nesting on the South Uist machair. *Bird Study* 25: 198-206

Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. & Tucker, B.W. 1940. *The Handbook of British Birds*, Vol. 4. Witherby, London

Appendix 1. Numbers of each type of prey seen during observations of feeding rates of Ringed and Grey Plovers at Lindisfarne

In the following tables, pecks and prey identified are listed for each month and separated according to species and area.

APPENDIX TABLE 1.1 DIET OF GREY PLOVERS ON THE LOW FLATS

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	-	-	0	1	0	2	4	0	3	0	3	-
Total pecks	-	-	166	266	167	336	505	21	470	99	236	-
Prey of which all sizes should be visible:												
Arenicola (whole)	-	-	2	1	0	1	2	0	6	4	10	-
Arenicola (tails)	-	-	0	0	0	5	1	0	0	0	2	-
Ragworm	-	-	0	0	0	0	0	0	1	0	0	-
Crabs	-	-	0	1	0	1	1	0	0	0	0	-
Algae	-	-	0	1	0	1	14	2	5	0	1	-
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	-	-	68	101	54	116	129	8	233	8	71	-
Mollusca (*Macoma, Hydrobia, Littorina*)	-	-	3	0	0	0	10	2	2	2	2	-
Other Crustacea	-	-	0	1	0	0	6	0	0	0	0	-
Successful pecks: prey not identified	-	-	51	98	63	60	109	4	54	3	98	-
Unsuccessful pecks	-	-	0	0	0	0	0	0	0	0	1	-
Pecks of unknown outcome	-	-	42	63	50	152	233	5	169	82	51	-

APPENDIX TABLE 1.2 DIET OF GREY PLOVERS ON THE HIGH FLATS

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	-	-	-	0	0	0	1	0	0	0	0	-
Total pecks	0	0	0	185	133	163	182	464	86	72	33	0
Prey of which all sizes should be visible:												
Arenicola (whole)	-	-	-	3	4	2	2	15	9	1	8	-
Arenicola (tails)	-	-	-	1	0	0	2	3	3	0	0	-
Ragworm	-	-	-	-	-	-	-	-	-	-	-	-
Crabs	-	-	-	1	0	1	0	1	0	0	0	-
Algae	-	-	-	1	0	5	7	35	4	0	0	-
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	-	-	-	31	65	22	55	116	10	5	4	-
Mollusca (*Macoma*, *Hydrobia*, *Littorina*)	-	-	-	2	1	0	2	18	3	0	0	-
Other Crustacea	-	-	-	0	0	0	0	1	0	0	0	-
Successful pecks: prey not identified	-	-	-	56	25	49	38	127	30	7	8	-
Unsuccessful pecks	-	-	-	1	0	0	0	1	0	0	1	-
Pecks of unknown outcome	-	-	-	89	38	84	76	147	27	59	12	-

APPENDIX TABLE 1.3 DIET OF GREY PLOVERS ON AREAS OF LINDISFARNE AWAY FROM HOLY ISLAND SANDS

	North Shore			Other areas	
	D	J	F	M	A
Aborted pecks	0	0	0	0	0
Total pecks	31	32	31	59	30
Prey of which all sizes should be visible:					
Arenicola (whole)	0	0	0	3	0
Arenicola (tails)	0	0	0	0	0
Ragworms	-	-	-	-	-
Crabs	2	0	0	0	0
Algae	0	1	0	0	0
Prey of which not all sizes visible:					
Thin worms (principally *Notomastus*)	2	9	1	13	2
Mollusca (*Macoma*, *Hydrobia*, *Littorina*)	0	0	1	0	0
Other Crustacea	0	0	0	0	0
Successful pecks; prey not identified	19	3	6	4	23
Unsuccessful pecks	0	0	0	0	0
Pecks of unknown outcome	8	19	23	39	5

APPENDIX TABLE 1.4 DIET OF RINGED PLOVERS ON THE LOW FLATS

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	-	0	0	1	0	0	1	0	0	-	-	0
Total pecks	-	437	845	745	263	307	1221	80	926	-	-	75
Prey of which all sizes should be visible:												
Arenicola (whole)	-	1	0	0	0	0	3	0	0	-	-	0
Arenicola (tails)	-	1	0	0	0	0	2	0	2	-	-	0
Ragworm	-	-	-	-	-	-	-	-	-	-	-	-
Crabs	-	0	0	0	0	0	0	0	0	-	-	0
Algae	-	1	0	0	1	2	7	2	1	-	-	0
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	-	66	92	163	70	59	335	30	242	-	-	6
Mollusca (*Macoma*, *Hydrobia*, *Littorina*)	-	0	0	0	0	0	2	0	1	-	-	0
Other Crustacea	-	0	0	3	0	0	8	0	0	-	-	0
Successful pecks: prey not identified	-	264	257	234	73	57	389	31	189	-	-	43
Unsuccessful pecks	-	0	0	0	0	0	0	0	1	-	-	0
Pecks of unknown outcome	-	104	496	345	119	189	475	17	490	-	-	26

APPENDIX TABLE 1.5 DIET OF RINGED PLOVERS ON THE HIGH FLATS

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	-	0	0	1	0	0	0	0	0	0	-	-
Total pecks	-	52	196	559	160	38	720	186	151	757	-	-
Prey of which all sizes should be visible:												
Arenicola (whole)	-	0	2	0	0	0	4	0	1	0	-	-
Arenicola (tails)	-	0	0	0	0	0	28	0	0	0	-	-
Ragworm	-	-	-	-	-	-	-	-	-	-	-	-
Crabs	-	0	0	0	1	0	0	0	0	0	-	-
Algae	-	0	0	3	1	0	3	0	0	2	-	-
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	-	0	3	27	25	2	13	8	1	33	-	-
Mollusca (*Macoma, Hydrobia, Littorina*)	-	0	0	0	0	0	1	1	0	0	-	-
Other Crustacea	-	0	4	0	0	0	1	0	0	0	-	-
Sandhoppers	-	0	0	0	0	0	0	0	0	3	-	-
Successful pecks: prey not identified	-	50	101	228	41	4	136	11	47	525	-	-
Unsuccessful pecks	-	0	1	0	0	0	0	0	0	0	-	-
Pecks of unknown outcome	-	2	85	296	92	32	534	166	102	194	-	-

APPENDIX TABLE 1.6 DIET OF FULLY GROWN RINGED PLOVERS ON THE NORTH SHORE

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	1	1	0	-	-	0	0	0	0	0	0	0
Total pecks	421	731	22	-	-	96	208	195	1201	1319	242	187
Prey of which all sizes should be visible:												
Arenicola (whole)	7	18	0	-	-	0	0	1	2	5	1	0
Arenicola (tails)	0	0	0	-	-	0	0	0	5	4	1	0
Crabs	1	0	0	-	-	0	0	0	0	0	0	0
Algae	1	2	0	-	-	0	0	0	5	6	1	0
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	41	55	0	-	-	5	17	15	240	111	19	9
Mollusca (*Macoma*, *Hydrobia*, *Littorina*)	2	0	0	-	-	1	0	0	0	1	0	0
Other Crustacea (non-crab)	0	0	0	-	-	0	0	0	0	21	1	0
Sandhoppers	1	1	0	-	-	0	0	0	0	0	0	0
Fly	2	4	0	-	-	0	0	0	0	3	0	0
Successful pecks: prey not identified	188	224	12	-	-	19	28	39	144	554	122	85
Unsuccessful pecks	0	0	0	-	-	0	0	0	0	1	0	0
Pecks of unknown outcome	178	427	10	-	-	71	163	140	805	613	97	93

APPENDIX TABLE 1.7 DIET OF FULLY GROWN RINGED PLOVERS ON AREAS OF LINDISFARNE NNR AWAY FROM HOLY ISLAND SANDS AND THE NORTH SHORE

	J	A	S	O	N	D	J	F	M	A	M	J
Aborted pecks	0	0	-	-	-	-	-	-	0	0	-	0
Total pecks	349	691	-	-	-	-	-	-	122	444	-	9
Prey of which all sizes should be visible:												
Arenicola (whole)	1	5	-	-	-	-	-	-	0	0	-	0
Arenicola (tails)	0	1	-	-	-	-	-	-	0	0	-	0
Ragworm	0	0	-	-	-	-	-	-	0	0	-	2
Crabs	0	0	-	-	-	-	-	-	0	0	-	0
Algae	0	0	-	-	-	-	-	-	0	0	-	0
Prey of which not all sizes visible:												
Thin worms (principally *Notomastus*)	8	40	-	-	-	-	-	-	0	18	-	0
Mollusca (*Macoms*, *Hydrobia*, *Littorina*)	0	0	-	-	-	-	-	-	0	0	-	0
Other crustacea (non-crab)	0	1	-	-	-	-	-	-	0	0	-	0
Sandhoppers	3	4	-	-	-	-	-	-	0	0	-	0
Fly	3	0	-	-	-	-	-	-	0	0	-	0
Successful pecks: prey not identified	205	413	-	-	-	-	-	-	2	102	-	0
Unsuccessful pecks	0	0	-	-	-	-	-	-	0	0	-	0
Pecks of unknown outcome	129	227	-	-	-	-	-	-	120	324	-	7

Appendix 2. Sizes of thin red worms seen to be taken during observations of feeding rates of Ringed and Grey Plovers at Lindisfarne

In the following tables, the number of thin red worms (principally *Notomastus*) of each length category are listed for each month and separated according to species and locality.

Length is stretched length as the worm is pulled from the substratum, and is recorded in relation to the height of bill above the ground (about 80 mm for Ringed Plover and 120 mm for Grey Plover).

APPENDIX TABLE 2.1 LENGTHS OF THIN RED WORMS SEEN TO BE TAKEN BY GREY PLOVERS

(a) LOW FLATS

Length (xbill-height)	J	A	S	O	N	D	J	F	M	A	M	J
< ¼	-	-	12	34	23	46	51	2	93	1	19	-
¼	-	-	23	22	16	14	19	0	30	0	17	-
½	-	-	13	19	6	22	21	3	49	0	19	-
¾	-	-	7	3	2	2	14	0	9	0	5	-
1	-	-	5	10	2	12	12	2	14	1	4	-
1¼	-	-	7	5	0	7	6	1	6	0	3	-
1½	-	-	1	7	0	3	0	0	5	1	2	-
1¾	-	-	0	1	0	0	0	0	0	0	1	-
2	-	-	0	0	0	0	2	0	0	0	0	-
>2	-	-	0	0	0	0	0	0	0	0	0	-
Total	-	-	68	101	49	106	125	8	206	3	70	-

(b) HIGH FLATS

< ¼	-	-	-	25	27	16	22	79	5	1	3	-
¼	-	-	-	1	5	0	1	4	2	0	1	-
½	-	-	-	0	10	3	9	10	1	0	0	-
¾	-	-	-	0	5	0	1	2	0	0	0	-
1	-	-	-	0	11	0	8	2	1	0	0	-
1¼	-	-	-	0	5	0	1	0	0	0	0	-
1½	-	-	-	0	0	0	0	0	0	0	0	-
1¾	-	-	-	0	0	0	0	0	0	0	0	-
2	-	-	-	0	0	0	0	0	0	0	0	-
>2	-	-	-	0	0	0	0	0	0	0	0	-
Total	-	-	-	26	63	19	42	97	9	1	4	-

(c) OTHER AREAS

< ¼						2	6	1	12	1		
¼						0	0	0	0	1		
½						0	0	0	1	0		
¾						0	0	0	0	0		
1						0	0	0	0	0		
1¼						0	0	0	0	0		
1½						0	2	0	0	0		
1¾						0	0	0	0	0		
2						0	0	0	0	0		
>2						0	0	0	0	0		
Total						2	8	1	13	2		

APPENDIX TABLE 2.2 LENGTHS OF THIN RED WORMS SEEN TO BE TAKEN BY RINGED PLOVERS AT LINDISFARNE

(a) LOW FLATS

Length (xbill-height)	J	A	S	O	N	D	J	F	M	A	M	J
< ¼	-	18	35	56	35	40	155	18	138	-	-	0
¼	-	6	14	10	11	2	25	1	6	-	-	0
½	-	10	8	27	10	4	37	4	33	-	-	0
¾	-	5	2	8	2	3	22	2	5	-	-	0
1	-	7	10	29	5	5	55	2	44	-	-	0
1¼	-	6	5	2	1	0	11	0	4	-	-	0
1½	-	9	3	19	0	1	12	3	6	-	-	0
1¾	-	1	0	2	0	0	1	0	0	-	-	0
2	-	2	8	6	1	0	6	0	2	-	-	0
>2	-	1	3	1	0	0	0	0	0	-	-	0
Total	-	65	88	160	65	55	324	30	238	-	-	0

(b) HIGH FLATS

< ¼	-	0	2	14	18	1	7	4	1	18	-	-
¼	-	0	0	1	1	0	2	0	0	5	-	-
½	-	0	0	7	3	0	1	0	0	5	-	-
¾	-	0	0	1	0	0	0	0	0	2	-	-
1	-	0	1	2	1	0	1	3	0	2	-	-
1¼	-	0	0	0	0	0	0	0	0	0	-	-
1½	-	0	0	0	0	0	0	0	0	0	-	-
1¾	-	0	0	0	0	0	0	0	0	0	-	-
2	-	0	0	0	0	0	0	0	0	0	-	-
>2	-	0	0	0	0	0	0	0	0	0	-	-
Total	-	0	3	25	23	1	11	7	1	32	-	-

APPENDIX TABLE 2.2 CONTINUED

(c) NORTH SHORE

Length (xbill-height)	J	A	S	O	N	D	J	F	M	A	M	J
< ¼	25	26	0	-	-	5	12	8	148	55	15	4
¼	1	6	0	-	-	0	0	0	4	16	1	1
½	8	13	0	-	-	0	2	1	27	14	1	2
¾	0	0	0	-	-	0	0	1	0	5	0	0
1	7	1	0	-	-	0	2	4	24	8	0	1
1¼	0	0	0	-	-	0	0	0	1	2	0	0
1½	0	0	0	-	-	0	1	0	0	2	0	0
1¾	0	0	0	-	-	0	0	0	0	0	0	0
2	0	0	0	-	-	0	0	0	0	0	0	0
>2	0	0	0	-	-	0	0	0	0	0	0	0
Total	41	46	0	-	-	5	17	14	204	102	17	8

(d) OTHER AREAS

< ¼	6	33	-	-	-	-	-	-	0	13	-	0
¼	0	0	-	-	-	-	-	-	0	1	-	0
½	1	3	-	-	-	-	-	-	0	1	-	0
¾	0	1	-	-	-	-	-	-	0	0	-	0
1	0	0	-	-	-	-	-	-	0	0	-	0
1¼	0	0	-	-	-	-	-	-	0	0	-	0
1½	0	0	-	-	-	-	-	-	0	0	-	0
1¾	0	0	-	-	-	-	-	-	0	0	-	0
2	0	0	-	-	-	-	-	-	0	0	-	0
>2	0	0	-	-	-	-	-	-	0	0	-	0
Total	7	37	-	-	-	-	-	-	0	15	-	0

Appendix 3. Computer handling of observations on plover foraging behaviour

This Appendix lists the two computer programs written to sort the observations on plover foraging behaviour (see Papers 2 & 1) and gives examples of the material input and output by these programs. The following material is presented:

1. list of data formats and codes;
2. listing of 'PLOVPROG';
3. listing of 'PLOVP2';
4. example of input of observations on duration of each activity;
5. example of input of observations on distances moved;
6. example of input of observations of frequencies of pecks and prey taken;
7. example of printed output from PLOVPROG for section-4-type input;
8. example of printed output from PLOVP2 for section-4-type input;
9. example of output to computer file (for subsequent analysis, e.g. by SPSS) from PLOVPROG (output from PLOVP2 uses the same format).

SECTION 1. DATA INPUT AND OUTPUT FORMATS

Each observation of each foraging bird (usually about 2 minutes duration but not restricted to this) is referred to here as a 'case'. PLOVPROG and PLOVP2 read data as cards (or card images). For any form of data, the first 70 columns of the first card of each case follows the same format. This is defined below and examples can be seen in sections 4, 5 and 6.

First card columns	entries (all numerical data are right-justified within each field)
1 - 4	Case serial number.
5 - 6	Card serial number (always 01 for 'first card').
7 - 8	Number of continuation cards for this case.
9	Medium; 1 = timed data; 2 = distance moved data; 5 = data on frequency only.
10	Species: 1 = Ringed Plover; 2 = Grey Plover; 3 = Dunlin; 4 = Sanderling; 5 = Golden Plover; 6 = Lapwing; 7 = Curlew.

11 Sex; 0 = unknown; 1 = male; 2 = female.

12 Age; (follows Euring code); 1 = pullus (i.e. not yet fledged); 2 = fully grown but age totally unknown; 3 = hatched during current calender year; 4 = hatched before current calender year, exact year unknown; 5 = hatched during previous calender year; 6 = hatched before last calender year; 7 = hatched 2 calender years ago; 8 = hatched 3 or more calender years ago.

13 - 14 Age of chick in days. For older birds or chicks of unknown age: -1.

15 Foot-vibration: 0 = not recorded; 1 = none; 2 = foot-vibration throughout observation case; 3 = foot-vibration for part of time.

16 - 18 Distance to nearest bird of same species in metres; -1 = unrecorded; 100 = distant.

19 - 21 Distance to nearest other bird, coded as above.

22 - 24 Number of conspecifics in flock: 1 = bird alone; 0 = unrecorded.

25 Position in flock: 0 = unrecorded; 1 = centre; 2 = intermediate; 3 = edge.

26 - 27 Locality

01	N Shore - Tip	18	Flats above P.W.,hollows
02	N Shore - Barrier	19	Flats above P.W.,ridges
03	N Shore - East	20	Ringed Plover Gully
04	N Shore - West	21	Grey Plover Flats
05	Snook Point	22	Godwit Creek
06	Rig off Snook Point	23	West of Godwit Creek
07	Rig off N Shore	24	Sandon Bay
08	Goswick Flats	25	Harbour
09	Goswick Rig	26	Tealhole
10	Goswick Sea Shore	27	Fenham-le-Moor
11	By Causeway, W of Channel	28	Fenham Mill
12	By Causeway, E of Channel	29	Elwick
13	Snook House Bay	30	Wideopens
14	High flats below Tip	31	Old Law, inner
15	By Road, Tip	32	Old Law, Guile Point
16	By Road, Small Saltmarsh	33	Old Law, outer
17	Flats above Pilgrims' Way, High Gully	34	Ross Links, North

	35 Ross Links, South	53 North End Runway
	36 Budle Bay	54 S W of Radio Hut
		55 Noret Shore
	51 Tunnelelv	56 E of mid Runway
	52 South Runway	57 By Nyhavn Road

28 Status: 1 = on territory; otherwise 0

29 - 32 Time: 24 h clock

33 - 38 Date: numerical, in sequence day, month, year, 2 digits for each.

39 Rainfall during case: 0 = none; 1 = light drizzle; 2 = drizzle; 3 = light rain; 4 = rain; 5 = heavy rain; 6 = downpour; 7 = hail; 8 = sleet; 9 = snow.

40 Cloud cover: in eighths of the sky covered, plus 9 = ground level mist with full cover (although observations in such conditions were rare!)

41 - 42 Windforce (Beaufort Scale)

43 Wind direction: 0 = unrecorded or none; 1 = N; 2 = NE; 3 = E; 4 = SE; 5 = S; 6 = SW; 7 = W; 8 = NW.

44 - 46 Air temperature, entered in tenths of degrees Centigrade.

47 - 49 Sand temperature, as above.

50 - 53 Predicted time of high water preceding observation (24 h clock).

54 - 56 Predicted height at Leith of preceding high water (tenths of metres).

57 - 60 Predicted time of high water following observation.

61 - 63 Predicted height at Leith of following high water.

64 - 67 Individual, if known. Colour-ringed individuals were entered using the last four digits of their metal ring numbers. Other codes were used for other, temporarily identifiable birds, such as the male of a particular territory or unringed chicks of a particular family.

68 - 69 Species of nearest other bird: 0 = unrecorded or none; 1 = Ringed Plover; 2 = Grey Plover; 3 = Dunlin; 4 = Oystercatcher; 5 = Bar-tailed Godwit; 6 = Redshank; 7 = Golden Plover; 8 = Turnstone; 9 = Lapwing; 10 = Curlew; 11 = Knot; 12 = Sanderling.

70 Substrate wetness and daylight conditions: 0 = daylight; 1 = dry, daylight; 2 = wet, daylight; 4 = dry, twilight; 5 = wet, twilight; 6 = dry, darkness; 7 = wet, darkness; 8 = twilight; 9 = darkness.

The format of continuation cards differs according to column 9 (Medium) of the first card. The three types are described below. For all sorts of data, the end of the batch (which usually consisted of about 50 cases) is indicated by a card with '-109' in the first four spaces.

Continuation cards for timed data

For all cards, columns 1 - 4 contain the case number and columns 5 - 6 the serial number of the card within the case. Columns 9 to 80 are divided into 9 fields of 8. Within each field the first four spaces were allocated to a code indicating activity and prey type and size if taken (left-justified), and the second four to the duration of this activity in tenths of a second (right-justified). An example of several cases is given in section 4. As many continuation cards as required are used. 'STOP' is entered in the first part of the field after the last activity in the case. The activity codes are listed below.

U = wait in up position

D = wait in down position

R = run

TN= turn (without running - this was infrequently recorded and the program recodes this as R)

DR= produce faecal dropping

PE= produce regurgitated pellet

DRI=drink

P = peck

PSU=peck, successful (prey seen to be taken, not identified)

PSM=peck small prey taken

PA =peck, *Arenicola* taken

PW =peck, thin worm of unknown length taken

PRO=peck, thin worm, shorter than $\frac{1}{4}$ bill-height taken

PR1 - 9 = similar to above for thin worms $\frac{1}{4}, \frac{1}{2}, \frac{3}{4}, 1, 1\frac{1}{4}, 1\frac{1}{2}, 1\frac{3}{4}, 2, >2$ times bill height, respectively.

PWE=peck at weed (algae)

PAB=aborted peck

SP = stop feeding to preen

SB =stop feeding to bathe

SR =stop feeding to roost

SS =stop feeding to stand
SD =stop feeding to display
SI =stop feeding to incubate or brood (or be brooded, for chick)

Continuation cards for data on distances moved

These data are recorded in the same way as for timed data, with the following exceptions:

(i) two fields of 4 digits each are added in columns 71 - 74 and 75 - 78 of the first card. These included the total time duration for the case and the amount of time actually foraging (in tenths of a second). (These two times differ if any of the activities coded with an initial S occur.)

(ii) On the continuation cards, the numbers of paces moved, instead of the time taken to make the run, are coded for each 'run'. For all other activities, the activity code is entered but the numerical component is recorded as zero.

Examples are given in Section 5.

Continuation cards for data on frequencies of prey, etc. only

For such data the first card is coded as for data on distances moved (except column 9).

Only one continuation card is used for each case. This records the case numbers in columns 1 - 4 and '02' in columns 5 - 6. Columns 7 to 75 are divided into 23 fields of 3. These are used to record (each right-justified) the frequencies in the case of the following activities, respectively: DR,PE,DRI,U,D,R,P,PSU,PSM,PA,PW,PRO,PR1,PR2, PR3,PR4,PR5,PR6,PR7,PR8,PR9,PWE,PAB.
Examples are given in Section 6.

Printed output

Apart from carrying out various checks on the data coding, sorting the data and storing it for further analysis, PLOVPROG and PLOVP2 print some basic statistics for manual checking and for some simple analyses. Examples are shown in Sections 7 and 8. PLOVP2 output differs from that of PLOVPROG by listing the recoded data used in the sorting. (For details of the recoding, see Paper 2.)

Output for storage and further analysis

Both programs store the sorted data for each case on disk-files (and also list these on a printer for manual checking). These disk-files were later grouped into a smaller number of files and stored on magnetic tape. An example of the format is given in Section 9.

For each case, the first line consists of an image of the first card (as for timed data input). The second line, labelled with case number and 'card' number 71, lists total time duration of case (sec); time spent foraging (sec); no. of droppings produced; no. of pellets produced; no. of drinks taken; total number of thin worms taken; and total number of pecks of any outcome made. There follow 15 further lines, labelled with case number and 'card' numbers 72 to 86 respectively. Each line carries the following three parameters for four variables; frequency within the case, sum of durations (or of paces for distance data), and sum of squares of durations (or of paces). The 60 variables represent activities or simple sequences of activities, these being (listed in order of occurrence in the file):

U-D; U-R; U-P; U-PSU; U-PSM; U-PA; U-PW; U-PR;
U-PWE; U-PAB; U; D; R-U; R-D; R-P; R-PSU;
R-PSM; R-PA; R-PW; R-PR; R-PWE; R-PAB; R; P;
PSU; PSM; PA; PW; PRO; PR1; PR2; PR3;
PR4; PR5; PR6; PR7; PR8; PR9; PWE; PAB;
P-U; PSU-U; PSM-U; PA-U; PW-U; PRA-U; PRB-U; PRC-U;
PWE-U; PAB-U; P-R; PSU-R; PSM-R; PA-R; PW-R; PRA-R;
PRB-R; PRC-R; PWE-R; PAB-R.

In the case of sequences, durations are summed for the element underlined in the above listing (e.g. PA-U refers to frequencies of this sequence, the sum of duration of those U's preceded by PA and the sums of squares of these durations). Apart from codes defined above, PR = peck, taking thin worm of any size, and PRA, PRB and PRC = peck taking thin worms of the regrouped categories PRO & PR1, PR2 to PR4, and PR5 to PR9, respectively.

SECTION 2. LISTING OF 'PLOVPROG'

```
      $COMPILE TIME=30
      C
      C                                  PLOVPROG
      C                                  ========
      C
      C     AUTHOR: M W PIENKOWSKI                    PROGRAM WRITTEN  APRIL 1975
      C     THIS LISTING INCORPORATES MODIFICATIONS UP TO SEPTEMBER 1979
      C
      C     A PROGRAM TO SORT SEQUENTIAL PLOVER FORAGING BEHAVIOUR BASED ON
      C     TIME OR DISTANCE MOVED, TO PRINT BASIC STATISTICS FOR EACH CASE,
      C     AND TO FILE SORTED DATA FOR EACH CASE; ALSO TO ADAPT SIMPLER DATA
      C     ON NUMBERS OF EACH ACTIVITY PER TIME TO THE SAME FORMAT FOR FILE
      C     STORAGE.
      C
      C     THE PROGRAM IS WRITTEN IN FORTRAN IV LANGUAGE AS ACCEPTED BY THE
      C     COMPILER *WATFIV; SLIGHT MODIFICATION WOULD BE NECESSARY FOR USE
      C     WITH OTHER FORTRAN COMPILERS. CARDS (OR CARD IMAGES) ARE READ ON
      C     LOGICAL UNIT 5; BASIC CASE STATISTICS ARE PRINTED ON LOGICAL UNIT
      C     6; AND SORTED DATA ARE OUTPUT ON LOGICAL UNIT 7.
      C
      C
            DIMENSION NACT(999),T(999),TUD(99),TUR(99),TUP(99),TUPSU(99),TUPSM
           1(99),TUPA(99),TUPW(99),TUPR(99),TDU(99),TDR(99),TDPSU(99),TDPSM(99
           2),TDPA(99),TDPW(99),TDPR(99),TRU(99),TRD(99),TRP(99),TRPSU(99),TRP
           3SM(99),TRPA(99),TRPW(99),TRPR(99),       TPSU(99),TPSM(99),TPA(99)
           4,TPW(99),TPR0(99),TPR1(99),TPR2(99),TPR3(99),TPR4(99),TPR5(99),TPR
           56(99),TPR7(99),TPR8(99),TPR9(99),        TPD(99),       TPSUU(99)
           6,TPSUD(99),TPSUR(99),TPSMU(99),TPSMD(99),TPSMR(99),TPAU(99),TPAD(9
           79),TPAR(99),TPWU(99),TPWD(99),TPWR(99),TPRAU(99),TPRAD(99),TPRAR(9
           89),TPRBU(99),TPRBD(99),TPRBR(99),TPRCU(99),TPRCD(99),TPRCR(99)
            DIMENSION TP(200),TPU(200),TPR(200)
            DIMENSION TUPWE(99),TUPAB(99),TDPWE(99),TDPAB(99),TRPWE(99),TRPAB(
           199),TPAB(99),TPABU(99),TPABD(99),TPABR(99),TPWE(99),TPWEU(99),TPWE
           2D(99),TPWER(99)
            DIMENSION TOP(99)
            DIMENSION TV(9999),TD(999),TR(999)
            COMMON FEEDT
            REAL MTI,MT2
            INTEGER HW1,HW2
            INTEGER ALL
            INTEGER PRA,PRB,PRC
            INTEGER U,D,R,DR,SP,SB,SR,SS,P,PSU,PSM,PA,PW,PR0,PR1,PR2,PR3,PR4,P
           1R5,PR6,PR7,PR8,PR9
            INTEGER PAB,PWE,PE,TN,SI,SD,ORI
            INTEGER PR
            INTEGER STOP
            DATA STOP/4HSTOP/
            DATA U,D,R,DR,SP,SB,SR,SS,P,PSU,PSM,PA,PW,PR,PRA,PRB,PRC,PR1,PR2,P
           1R3,PR4,PR5,PR6,PR7,PR8,PR9/1HU,1HD,1HR,2HDR,2HSP,2HSB,2HSR,2HSS,1H
           2P,3HPSU,3HPSM,2HPA,2HPW,2HPR,3HPRA,3HPRB,3HPRC,3HPR1,3HPR2,3HPR3,3
           3HPR4,3HPR5,3HPR6,3HPR7,3HPR8,3HPR9/
            DATA PWE,PAB,PE,SI,SD,ORI/3HPWE,3HPAB,2HPE,2HSI,2HSD,3HORI/
            DATA PR0/3HPR0/
            DATA TN/2HTN/
            DATA ALL/3HALL/
            DATA MCD,MCI,MTD,MTT,M,MF,MN,MNE,ME,MSE,MS,MSW,MW,MNW/4HC/DI,4HC/T
           1I,4HT/DI,4HT/TI,1HM,1HF,1HN,2HNE,1HE,2HSE,1HS,2HSW,1HW,2HNW/
            DATA MTN/4HT/NO/
      C
      C
      C
      C       INPUT DATA
      C
      C
          1 READ(5,101)NCASE,NSER,NC,MEDIUM,MSP,NSEX,NAGE,NDAYS,NFOOT,NDIST,ND
           1IST2,NFLOCK,NPOS,LOC,NSTAT,NTIM,NDATE,NRAIN,NCLOUD,NWIND,NDIR,AIRT
           2,AMUDT,HW1,HTI,HW2,HT2,INDIV,NEARSP,NWET,ZTT,ZFT
            IF(NCASE.EQ.-109)STOP
            IF(MEDIUM.EQ.5)GOTO 3010
            DO 10 I=1,NC
            NL=9*I-8
            NH=9*I
         10 READ(5,100)(NACT(J),T(J),J=NL,NH)
        101 FORMAT(14,12,12.4(1X,I2,1X,313.1X,I2,1X,I4,16.1,1X,I1,1X,I2,1X,F3.0,F3.0
           1,14,F3.0,14,F3.0,14,12,1X,2F4.0)
        100 FORMAT(8X,9(A4,F4.0))
            IF(MEDIUM.NE.2)GOTO 9010
            ITOP=NC*9
            DO 9011 I=1,ITOP
            T(I)=T(I)*10
       9011 CONTINUE
       9010 IF(MEDIUM.EQ.1)MMED=MTT
            IF(MEDIUM.EQ.2)MMED=MTD
            IF(MEDIUM.EQ.3)MMED=MCT
            IF(MEDIUM.EQ.4)MMED=MCD
            IF(MEDIUM.EQ.5)MMED=MTN
            MC=NC+1
            NCARD=NCASE
            WRITE(6,3000)NCASE,MC,MMED
       3000 FORMAT(1H1,9HCASE NO. ,I4,3H . ,I2,23H INITIAL DATA CARDS.   ,A4)
            IF(MSP.EQ.1)GOTO 3001
            IF(MSP.EQ.2)GOTO 3002
            IF(MSP.EQ.3)GOTO 3011
            IF(MSP.EQ.4)GOTO 3013
            IF(MSP.EQ.5)GOTO 3016
            IF(MSP.EQ.6)GOTO 3017
            WRITE(6,3020)MSP
       3020 FORMAT(12HOSPECIES NO.,I4)
       3001 WRITE(6,3003)
       3003 FORMAT(14HORINGED PLOVER)
            GOTO 3004
       3002 WRITE(6,3005)
       3005 FORMAT(12HOGREY PLOVER)
            GOTO 3004
       3011 WRITE(6,3012)
       3012 FORMAT(7HODUNLIN)
            GOTO 3004
       3016 WRITE(6,3018)
       3018 FORMAT(14HOGOLDEN PLOVER)
            GOTO 3004
       3017 WRITE(6,3019)
       3019 FORMAT(8HOLAPWING)
            GOTO 3004
       3013 WRITE(6,3014)
       3014 FORMAT(11HOSANDERLING)
       3004 CONTINUE
            WRITE(6,4000)INDIV
       4000 FORMAT(15H INDIVIDUAL NO.,I4)
            RAIRT=AIRT/10
            RAMUDT=AMUDT/10
            MTI=HTI/10
```

```
      MT2=HT2/10
      IF(NSEX.EQ.0)MSEX=0
      IF(NSEX.EQ.1)MSEX=M
      IF(NSEX.EQ.2)MSEX=MF
      WRITE(6,3006)MSEX,NAGE,NDAYS,NSTAT,LOC,NTIM,NDATE
 3006 FORMAT(4H SEX,A4,12H,  AGE CODE ,I1,12H (CHICK AGE ,I2,16H DAYS),
     1STATUS: ,I1,17H, LOCATION CODE: ,I2,8H, TIME: ,I4,8H, DATE: ,I6)
      IF(NDIR.EQ.0)MDIR=0
      IF(NDIR.EQ.1)MDIR=MN
      IF(NDIR.EQ.2)MDIR=MNE
      IF(NDIR.EQ.3)MDIR=ME
      IF(NDIR.EQ.4)MDIR=MSE
      IF(NDIR.EQ.5)MDIR=MS
      IF(NDIR.EQ.6)MDIR=MSW
      IF(NDIR.EQ.7)MDIR=MW
      IF(NDIR.EQ.8)MDIR=MNW
      WRITE(6,3007)NRAIN,NCLOUD,NWIND,MDIR,RAIRT,RAMUDT,HW1,MT1,HW2,MT2
 3007 FORMAT(12HOPAIN CODE: ,I1,9H, CLOUD: ,I1,16H/8, WIND FORCE: ,I2,6H
     1 FROM ,A4,12H, AIR TEMP: ,F4.1,18H, SUBSTRATE TEMP: ,F4.1,8H, HW A
     2T ,I4,3H ( ,F4.1,7H ) AND ,I4,3H ( ,F4.1,2H ))
      WRITE(6,3008)NFOOT,NOIST,NOIST2,NFLOCK,NPOS
 3008 FORMAT(1H ,11HFOOTSHAKE: ,I1,33H, DISTANCE FROM NEAREST SAME SP: ,
     1I3,14H M, OTHER SP: ,I3,16H M, FLOCK SIZE: ,I3,21H, POSITION IN FL
     2OCK: ,I1)
      IF(INDIV.EQ.0)GOTO 3010
      WRITE(6,3009)INDIV
 3009 FORMAT(21HOINDIVIDUAL CODE NO. ,I4)
 3010 CONTINUE
C
C
C       SET  ZEROS
C
C
      NDROP=0
      NUPWE=NUPAB=NDPWE=NDPAB=NRPWE=NRPAB=NPE=NSI=NSD=NPAB=NPABU=0
      NPABD=NPABR=NPWE=NPWEU=NPWED=NPWER=NDRI=NPU=NPD=NPR=NPSUU=0
      NPSUD=NPSUR=NPSMU=NPSMD=NPSMR=NPAU=NPAD=NPAR=NPWU=NPWD=NPWR=0
      NPRAU=NPRAD=NPRAR=NPRBU=NPRBD=NPRBR=NPRCU=NPRCD=NPRCR=0
      NU=ND=NR=NDR=NSP=NSB=NSR=NSS=NP=NPSU=NPSM=NPA=NPW=NPR0=NPR1=0
      NPR2=NPR3=NPR4=NPR5=NPR6=NPR7=NPR8=NPR9=NPRT=0
      TOTT=FEEDT=0.
      NUD=NUR=NUP=NUPSU=NUPSM=NUPA=NUPW=NUPR=NDU=NDR=NDPSU=NDPSM=0
      NDP=0
      NDPA=NDPW=NDPR=NRU=NRD=NRP=NRPSU=NRPSM=NRPA=NRPW=NRPR=0
      IF(MEDIUM.EQ.5)GOTO 6000
C
C
C         SORT FIRST ACTIVITIES
C
C
      I=1
      GOTO 76
   74 FEEDT=FEEDT+T(I)
   78 TOTT=TOTT+T(I)
   77 I=I+1
   76 IF(NACT(I).EQ.STOP)GOTO 75
C
C       ( GO TO CALCULATE AND PRINT OUT )
C
      IF(NACT(I).EQ.U)GOTO 50

      IF(NACT(I).EQ.D)GOTO 51
      IF(NACT(I).EQ.TN)NACT(I)=R
      IF(NACT(I).EQ.R)GOTO 52
      IF(NACT(I).EQ.DR)GOTO 53
      IF(NACT(I).EQ.PE)GOTO 81
      IF(NACT(I).EQ.SP)GOTO 54
      IF(NACT(I).EQ.SB)GOTO 55
      IF(NACT(I).EQ.SR)GOTO 56
      IF(NACT(I).EQ.SS)GOTO 57
      IF(NACT(I).EQ.SI)GOTO 79
      IF(NACT(I).EQ.SD)GOTO 80
      IF(NACT(I).EQ.P)GOTO 58
      IF(NACT(I).EQ.PSU)GOTO 59
      IF(NACT(I).EQ.PSM)GOTO 60
      IF(NACT(I).EQ.PA)GOTO 61
      IF(NACT(I).EQ.PW)GOTO 62
      IF(NACT(I).EQ.PR0)GOTO 63
      IF(NACT(I).EQ.PR1)GOTO 64
      IF(NACT(I).EQ.PR2)GOTO 65
      IF(NACT(I).EQ.PR3)GOTO 66
      IF(NACT(I).EQ.PR4)GOTO 67
      IF(NACT(I).EQ.PR5)GOTO 68
      IF(NACT(I).EQ.PR6)GOTO 69
      IF(NACT(I).EQ.PR7)GOTO 70
      IF(NACT(I).EQ.PR8)GOTO 71
      IF(NACT(I).EQ.PR9)GOTO 72
      IF(NACT(I).EQ.PAB)GOTO 82
      IF(NACT(I).EQ.PWE)GOTO 83
      IF(NACT(I).EQ.DRI)GOTO 84
      WRITE(6,201)I
  201 FORMAT(31HOUNRECOGNISED CODE AT ACTIVITY ,I4)
      GOTO 1
C
C       ( GO TO NEXT CASE )
C
C
C
C       FIRST ACTIVITY = U
C
C
   50 NU=NU+1
      K=0
      IF(NACT(I+1).NE.DR)GOTO 501
      K=1
      T(I)=T(I)+T(I+1)
  501 L=I+1+K
      TU(NU)=T(I)
      IF(NACT(L).EQ.D)GOTO 502
      IF(NACT(L).EQ.R.OR.NACT(L).EQ.TN)GOTO 503
      IF(NACT(L).EQ.P)GOTO 504
      IF(NACT(L).EQ.PSU)GOTO 505
      IF(NACT(L).EQ.PSM)GOTO 506
      IF(NACT(L).EQ.PA)GOTO 507
      IF(NACT(L).EQ.PW)GOTO 508
      IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
     1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
     2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 509
      IF(NACT(L).EQ.PWE)GOTO 500
      IF(NACT(L).EQ.PAB)GOTO 5000
      GOTO 74
```

```
      502 NUD=NUD+1
          TUD(NUD)=T(I)
          GOTO 74
      503 NUR=NUR+1
          TUR(NUR)=T(I)
          GOTO 74
      504 NUP=NUP+1
          TUP(NUP)=T(I)
          GOTO 74
      505 NUPSU=NUPSU+1
          TUPSU(NUPSU)=T(I)
          GOTO 74
      506 NUPSM=NUPSM+1
          TUPSM(NUPSM)=T(I)
          GOTO 74
      507 NUPA=NUPA+1
          TUPA(NUPA)=T(I)
          GOTO 74
      508 NUPW=NUPW+1
          TUPW(NUPW)=T(I)
          GOTO 74
      509 NUPR=NUPR+1
          TUPR(NUPR)=T(I)
          GOTO 74
      500 NUPWE=NUPWE+1
          TUPWE(NUPWE)=T(I)
          GOTO 74
     5000 NUPAB=NUPAB+1
          TUPAB(NUPAB)=T(I)
          GOTO 74
C
C
C       FIRST ACTIVITY = D  (DOWN)
C
C
       51 ND=ND+1
          K=0
          IF(NACT(I+1).NE.OR)GOTO 511
          K=1
          T(I)=T(I)+T(I+1)
      511 L=I+1+K
          TD(ND)=T(I)
          IF(NACT(L).EQ.U)GOTO 512
          IF(NACT(L).EQ.R.OR.NACT(L).EQ.TN)GOTO 513
          IF(NACT(L).EQ.P)GOTO 514
          IF(NACT(L).EQ.PSU)GOTO 515
          IF(NACT(L).EQ.PSM)GOTO 516
          IF(NACT(L).EQ.PA)GOTO 517
          IF(NACT(L).EQ.PW)GOTO 518
          IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
         1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
         2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 519
          IF(NACT(L).EQ.PWE)GOTO 510
          IF(NACT(L).EQ.PAB)GOTO 5100
          GOTO 74
      512 NDU=NDU+1
          TDU(NDU)=T(I)
          GOTO 74
      513 NDR=NDR+1
          TDR(NDR)=T(I)

          GOTO 74
      514 NDP=NDP+1
          TDP(NDP)=T(I)
          GOTO 74
      515 NDPSU=NDPSU+1
          TDPSU(NDPSU)=T(I)
          GOTO 74
      516 NDPSM=NDPSM+1
          TDPSM(NDPSM)=T(I)
          GOTO 74
      517 NDPA=NDPA+1
          TDPA(NDPA)=T(I)
          GOTO 74
      518 NDPW=NDPW+1
          TDPW(NDPW)=T(I)
          GOTO 74
      519 NDPR=NDPR+1
          TDPR(NDPR)=T(I)
          GOTO 74
      510 NDPWE=NDPWE+1
          TDPWE(NDPWE)=T(I)
          GOTO 74
     5100 NDPAB=NDPAB+1
          TDPAB(NDPAB)=T(I)
          GOTO 74
C
C
C       FIRST ACTIVITY = R ( OR T )        (RUN - OR TURN)
C
C
       52 NR=NR+1
          K=0
          IF(NACT(I+1).NE.OR)GOTO 521
          K=1
          T(I)=T(I)+T(I+1)
      521 L=I+1+K
          TR(NR)=T(I)
          IF(NACT(L).EQ.U)GOTO 522
          IF(NACT(L).EQ.D)GOTO 523
          IF(NACT(L).EQ.P)GOTO 524
          IF(NACT(L).EQ.PSU)GOTO 525
          IF(NACT(L).EQ.PSM)GOTO 526
          IF(NACT(L).EQ.PA)GOTO 527
          IF(NACT(L).EQ.PW)GOTO 528
          IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
         1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
         2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 529
          IF(NACT(L).EQ.PWE)GOTO 520
          IF(NACT(L).EQ.PAB)GOTO 5200
          GOTO 74
      522 NRU=NRU+1
          TRU(NRU)=T(I)
          GOTO 74
      523 NRD=NRD+1
          TRD(NRD)=T(I)
          GOTO 74
      524 NRP=NRP+1
          TRP(NRP)=T(I)
          GOTO 74
      525 NRPSU=NRPSU+1
```

```
361              TRPSU(NRPSU)=T(I)
362              GOTO 74
363           526 NRPSM=NRPSM+1
364              TRPSM(NRPSM)=T(I)
365              GOTO 74
366           527 NRPA=NRPA+1
367              TRPA(NRPA)=T(I)
368              GOTO 74
369           528 NRPW=NRPW+1
370              TRPW(NRPW)=T(I)
371              GOTO 74
372           529 NRPR=NRPR+1
373              TRPR(NRPR)=T(I)
374              GOTO 74
375           520 NRPWE=NRPWE+1
376              TRPWE(NRPWE)=T(I)
377              GOTO 74
378          5200 NRPAB=NRPAB+1
379              TRPAB(NRPAB)=T(I)
380              GOTO 74
381         C
382         C
383         C     FIRST ACTIVITY = DR  ( DROPPING )
384         C
385         C
386           53 NDROP=NDROP+1
387              GOTO 77
388         C
389         C
390         C       FIRST ACTIVITY = PE  ( PELLET )
391         C
392         C
393           81 NPE=NPE+1
394              GOTO 77
395         C
396         C
397         C       FIRST ACTIVITY = SP  ( STOP   PREEN )
398         C
399         C
400           54 NSP=NSP+1
401              REALT=TOTT/10.
402              REALT2=(TOTT+T(I))/10.
403              WRITE(6,202)REALT,REALT2
404          202 FORMAT(13H PREENING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
405              GOTO 78
406         C
407         C
408         C       FIRST ACTIVITY = SB  ( STOP    BATHE )
409         C
410         C
411           55 NSB=NSB+1
412              REALT=TOTT/10.
413              REALT2=(TOTT+T(I))/10.
414              WRITE(6,203)REALT,REALT2
415          203 FORMAT(12H BATHING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
416              GOTO 78
417         C
418         C
419         C       FIRST ACTIVITY = SR  ( STOP    ROOSTING )
420         C
421         C
422           56 NSR=NSR+1
423              REALT=TOTT/10.
424              REALT2=(TOTT+T(I))/10.
425              WRITE(6,204)REALT,REALT2
426          204 FORMAT(13H ROOSTING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
427              GOTO 78
428         C
429         C
430         C       FIRST ACTIVITY = SS  ( STOP    STANDING )
431         C
432         C
433           57 NSS=NSS+1
434              REALT=TOTT/10.
435              REALT2=(TOTT+T(I))/10.
436              WRITE(6,205)REALT,REALT2
437          205 FORMAT(13H STANDING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
438              GOTO 78
439         C
440         C
441         C       FIRST ACTIVITY = SI  ( STOP    INCUBATE OR BROOD )
442         C
443         C
444           79 NSI=NSI+1
445              REALT=TOTT/10.
446              REALT2=(TOTT+T(I))/10.
447              WRITE(6,206)REALT,REALT2
448          206 FORMAT(27H INCUBATING OR BROODING AT ,F5.1,14H SECONDS TILL ,F5.1,
449             18H SECONDS)
450              GOTO 78
451         C
452         C
453         C       FIRST ACTIVITY = SD  ( STOP    DISPLAY )
454         C
455         C
456           80 NSD=NSD+1
457              REALT=TOTT/10.
458              REALT2=(TOTT+T(I))/10.
459              WRITE(6,207)REALT,REALT2
460          207 FORMAT(15H DISPLAYING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
461              GOTO 78
462         C
463         C
464         C       FIRST ACTIVITY = P  ( PECK )
465         C
466         C
467           58 NP=NP+1
468              TP(NP)=T(I)
469              IF(NACT(I+1).EQ.U)GOTO 580
470              IF(NACT(I+1).EQ.D)GOTO 581
471              IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 582
472              GOTO 74
473          580 NPU=NPU+1
474              TPU(NPU)=T(I+1)
475              IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPU(NPU)=TPU(NPU)+T(I+2)
476              GOTO 74
477          581 NPD=NPD+1
478              TPD(NPD)=T(I+1)
479              IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPD(NPD)=TPD(NPD)+T(I+2)
480              GOTO 74
```

```
C
  582 NPR=NPR+1
      TPR(NPR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPR(NPR)=TPR(NPR)+T(I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PSU    (  PECK    SUCCESS )
C
C
   59 NPSU=NPSU+1
      TPSU(NPSU)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 590
      IF(NACT(I+1).EQ.D)GOTO 591
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 592
      GOTO 74
  590 NPSUU=NPSUU+1
      TPSUU(NPSUU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUU(NPSUU)=TPSUU(NPSUU)+T(
     1I+2)
      GOTO 74
  591 NPSUD=NPSUD+1
      TPSUD(NPSUD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUD(NPSUD)=TPSUD(NPSUD)+T(
     1I+2)
      GOTO 74
  592 NPSUR=NPSUR+1
      TPSUR(NPSUR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUR(NPSUR)=TPSUR(NPSUR)+T(
     1I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY  =  PSM    (  PECK    SMALL ITEM  )
C
C
   60 NPSM=NPSM+1
      TPSM(NPSM)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 600
      IF(NACT(I+1).EQ.D)GOTO 601
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 602
      GOTO 74
  600 NPSMU=NPSMU+1
      TPSMU(NPSMU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMU(NPSMU)=TPSMU(NPSMU)+T(
     1I+2)
      GOTO 74
  601 NPSMD=NPSMD+1
      TPSMD(NPSMD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMD(NPSMD)=TPSMD(NPSMD)+T(
     1I+2)
  602 NPSMR=NPSMR+1
      TPSMR(NPSMR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMR(NPSMR)=TPSMR(NPSMR)+T(
     1I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PA    ( PECK    ARENICOLA )
C
C


   61 NPA=NPA+1
      TPA(NPA)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 610
      IF(NACT(I+1).EQ.D)GOTO 611
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 612
      GOTO 74
  610 NPAU=NPAU+1
      TPAU(NPAU)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAU(NPAU)=TPAU(NPAU)+T(I+2)
      GOTO 74
  611 NPAD=NPAD+1
      TPAD(NPAD)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAD(NPAD)=TPAD(NPAD)+T(I+2)
      GOTO 74
  612 NPAR=NPAR+1
      TPAR(NPAR)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAR(NPAR)=TPAR(NPAR)+T(I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PW    ( PECK    WORM - UNIDENTIFIED )
C
C
   62 NPW=NPW+1
      TPW(NPW)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 620
      IF(NACT(I+1).EQ.D)GOTO 621
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 622
      GOTO 74
  620 NPWU=NPWU+1
      TPWU(NPWU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWU(NPWU)=TPWU(NPWU)+T(I+2)
      GOTO 74
  621 NPWD=NPWD+1
      TPWD(NPWD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWD(NPWD)=TPWD(NPWD)+T(I+2)
      GOTO 74
  622 NPWR=NPWR+1
      TPWR(NPWR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWR(NPWR)=TPWR(NPWR)+T(I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PR0-9    ( PECK    RED  WORM )
C
C
C       PR0    ( SMALL RED WORM )
C
   63 NPR0=NPR0+1
      TPR0(NPR0)=T(I)
      GOTO 630
C
C       PR1    ( 1/4 RED WORMS )
C
   64 NPR1=NPR1+1
      TPR1(NPR1)=T(I)
      GOTO 630
C
C    SMALL RED WORMS  ( PR0 & PR1 )
C
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```
      630 IF(NACT(I+1).EQ.U)GOTO 631
          IF(NACT(I+1).EQ.D)GOTO 632
          IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 633
          GOTO 74
      631 NPRAU=NPRAU+1
          TPRAU(NPRAU)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAU(NPRAU)=TPRAU(NPRAU)+T(
         1I+2)
          GOTO 74
      632 NPRAD=NPRAD+1
          TPRAD(NPRAD)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAD(NPRAD)=TPRAD(NPRAD)+T(
         1I+2)
          GOTO 74
      633 NPRAR=NPRAR+1
          TPRAR(NPRAR)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAR(NPRAR)=TPRAR(NPRAR)+T(
         1I+2)
          GOTO 74
C
C       PR2    ( 1/2 RED WORMS  )
C
       65 NPR2=NPR2+1
          TPR2(NPR2)=T(I)
          GOTO 650
C
C       PR3    ( 3/4 RED WORMS  )
C
       66 NPR3=NPR3+1
          TPR3(NPR3)=T(I)
          GOTO 650
C
C       PR4    (  1 RED WORMS  )
C
       67 NPR4=NPR4+1
          TPR4(NPR4)=T(I)
          GOTO 650
C
C       MEDIUM RED WORMS    ( PR2, PR3 & PR4  )
C
      650 IF(NACT(I+1).EQ.U)GOTO 651
          IF(NACT(I+1).EQ.D)GOTO 652
          IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 653
          GOTO 74
      651 NPR8U=NPR8U+1
          TPR8U(NPR8U)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPR8U(NPR8U)=TPR8U(NPR8U)+T(
         1I+2)
          GOTO 74
      652 NPR8D=NPR8D+1
          TPR8D(NPR8D)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPR8D(NPR8D)=TPR8D(NPR8D)+T(
         1I+2)
          GOTO 74
      653 NPR8R=NPR8R+1
          TPR8R(NPR8R)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAR(NPRAR)=TPRAR(NPRAR)+T(
         1I+2)
          GOTO 74
C
C       PR5    ( 1 1/4 RED WORMS  )
C
       68 NPR5=NPR5+1
          TPR5(NPR5)=T(I)
          GOTO 680
C
C       PR6    (  1 1/2 RED WORMS  )
C
       69 NPR6=NPR6+1
          TPR6(NPR6)=T(I)
          GOTO 680
C
C       PR7    (  1 3/4 RED WORMS  )
C
       70 NPR7=NPR7+1
          TPR7(NPR7)=T(I)
          GOTO 680
C
C       PR8    (  2 RED WORMS  )
C
       71 NPR8=NPR8+1
          TPR8(NPR8)=T(I)
          GOTO 680
C
C       PR9    (  >2 RED WORMS  )
C
       72 NPR9=NPR9+1
          TPR9(NPR9)=T(I)
          GOTO 680
C
C       LARGE RED WORMS    ( PR5, PR6, PR7, PR8 & PR9  )
C
      680 IF(NACT(I+1).EQ.U)GOTO 681
          IF(NACT(I+1).EQ.D)GOTO 682
          IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 683
          GOTO 74
      681 NPRCU=NPRCU+1
          TPRCU(NPRCU)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCU(NPRCU)=TPRCU(NPRCU)+T(
         1I+2)
          GOTO 74
      682 NPRCD=NPRCD+1
          TPRCD(NPRCD)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCD(NPRCD)=TPRCD(NPRCD)+T(
         1I+2)
          GOTO 74
      683 NPRCR=NPRCR+1
          TPRCR(NPRCR)=T(I+1)
          IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCR(NPRCR)=TPRCR(NPRCR)+T(
         1I+2)
          GOTO 74
C
C       FIRST ACTIVITY = PAB  ( PECK - ABORTED  )
C
C
       82 NPAB=NPAB+1
          TPAB(NPAB)=T(I)
          IF(NACT(I+1).EQ.U)GOTO 820
          IF(NACT(I+1).EQ.D)GOTO 821
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      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 822
      GOTO 74
  820 NPABU=NPABU+1
      TPABU(NPABU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABU(NPABU)=TPABU(NPABU)+T(
     1I+2)
      GOTO 74
  821 NPABD=NPABD+1
      TPABD(NPABD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABD(NPABD)=TPABD(NPABD)+T(
     1I+2)
      GOTO 74
  822 NPABR=NPABR+1
      TPABR(NPABR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABR(NPABR)=TPABR(NPABR)+T(
     1I+2)
      GOTO 74
C
C
C      FIRST ACTIVITY = PWE   ( PECK - WEED  )
C
C
   83 NPWE=NPWE+1
      TPWE(NPWE)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 830
      IF(NACT(I+1).EQ.D)GOTO 831
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 832
      GOTO 74
  830 NPWEU=NPWEU+1
      TPWEU(NPWEU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWEU(NPWEU)=TPWEU(NPWEU)+T(
     1I+2)
      GOTO 74
  831 NPWED=NPWED+1
      TPWED(NPWED)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWED(NPWED)=TPWED(NPWED)+T(
     1I+2)
      GOTO 74
  832 NPWER=NPWER+1
      TPWER(NPWER)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWER(NPWER)=TPWER(NPWER)+T(
     1I+2)
      GOTO 74
C
C
C      FIRST ACTIVITY = DRI   (  DRINK  )
C
C
   84 NDRI=NDRI+1
      GOTO 74
C
C
C       INITIAL TOTALLING CALCULATIONS
C
C
   75 IF(MEDIUM.EQ.2)FEEDT=ZFT*10.
      IF(MEDIUM.EQ.2)TOTT=ZTT*10.
      IF(FEEDT.EQ.0)GOTO 9000
      RATU=FLOAT(NU)/(FEEDT/600.)
      RATD=FLOAT(ND)/(FEEDT/600.)
      RATR=FLOAT(NR)/(FEEDT/600.)
      RATDR1=FLOAT(NDROP)/(FEEDT/600.)
      RATDR2=FLOAT(NDROP)/(TOTT/600.)
      RATPE1=FLOAT(NPE)/(FEEDT/600.)
      RATPE2=FLOAT(NPE)/(TOTT/600.)
      RATP=FLOAT(NP)/(FEEDT/600.)
      RATPSU=FLOAT(NPSU)/(FEEDT/600.)
      RATPSM=FLOAT(NPSM)/(FEEDT/600.)
      RATPA=FLOAT(NPA)/(FEEDT/600.)
      RATPW=FLOAT(NPW)/(FEEDT/600.)
      RATPA=FLOAT(NPA)/(FEEDT/600.)
      RATPR0=FLOAT(NPR0)/(FEEDT/600.)
      RATPR1=FLOAT(NPR1)/(FEEDT/600.)
      RATPR2=FLOAT(NPR2)/(FEEDT/600.)
      RATPR3=FLOAT(NPR3)/(FEEDT/600.)
      RATPR4=FLOAT(NPR4)/(FEEDT/600.)
      RATPR5=FLOAT(NPR5)/(FEEDT/600.)
      RATPR6=FLOAT(NPR6)/(FEEDT/600.)
      RATPR7=FLOAT(NPR7)/(FEEDT/600.)
      RATPR8=FLOAT(NPR8)/(FEEDT/600.)
      RATPR9=FLOAT(NPR9)/(FEEDT/600.)
      NPRT=NPR0+NPR1+NPR2+NPR3+NPR4+NPR5+NPR6+NPR7+NPR8+NPR9
      RATPRT=FLOAT(NPRT)/(FEEDT/600.)
      RATPWE=FLOAT(NPWE)/(FEEDT/600.)
      RATPAB=FLOAT(NPAB)/(FEEDT/600.)
      NPTOT=NP+NPSU+NPSM+NPA+NPW+NPRT+NPWE
      RATPTO=FLOAT(NPTOT)/(FEEDT/600.)
      RATDRI=FLOAT(NDRI)/(FEEDT/600.)
      GOTO 9001
 9000 RATU=RATD=RATR=RATDR1=RATPE1=RATP=0
      RATPSU=RATPSM=RATPA=RATPW=0
      RATPR0=RATPR1=RATPR2=RATPR3=RATPR4=0
      RATPR5=RATPR6=RATPR7=RATPR8=RATPR9=0
      RATPRT=RATPWE=RATPAB=RATPTO=RATDRI=0
 9001 REALTT=TOTT/10.
      REALFT=FEEDT/10.
      WRITE(6,1000)REALTT,REALFT
 1000 FORMAT(16H TIME ELAPSED = ,F5.1,20H      TIME FEEDING = ,F5.1)
      WRITE(6,1001)
 1001 FORMAT(1H0,9X,4X,1HU,4X,1HD,4X,1HR,2X,3HDRT,2X,3HDRF,2X,3HPET,2X,3
     1HPEF,4X,1HP,2X,3HPSU,2X,3HPSM,3X,2HPA,3X,2HPW)
      WRITE(6,1002)NU,ND,NR,NDROP,NDROP,NPE,NPE,NP,NPSU,NPSM,NPA,NPW
 1002 FORMAT(10H OBS. FREQ,14,11I5)
      WRITE(6,1003)RATU,RATD,RATR,RATDR1,RATDR2,RATPE1,RATPE2,RATP,RATPS
     1U,RATPSM,RATPA,RATPW
 1003 FORMAT(10H FREQ/MIN ,12F5.1)
      WRITE(6,1012)
 1012 FORMAT(1H0,9X,2X,3HPR0,2X,3HPR1,2X,3HPR2,2X,3HPR3,2X,3HPR4,2X,3HPR
     15,2X,3HPR6,2X,3HPR7,2X,3HPR8,2X,3HPR9,2X,3HPRT,2X,3HPWE,1X,4HPTOT,
     22X,3HPAB,2X,3HDRI)
      WRITE(6,1013)NPR0,NPR1,NPR2,NPR3,NPR4,NPR5,NPR6,NPR7,NPR8,NPR9,NPR
     1T,NPWE,NPTOT,NPAB,NDRI
 1013 FORMAT(10H OBS. FREQ,14,14I5)
      WRITE(6,1014)RATPR0,RATPR1,RATPR2,RATPR3,RATPR4,RATPR5,RATPR6,RATP
     1R7,RATPR8,RATPR9,RATPRT,RATPWE,RATPTO,RATPAB,RATDRI
 1014 FORMAT(10H FREQ/MIN ,15F5.1)
C
C
C       STATISTICS OUTPUT
C
```

```
      C
            WRITE(6,1004)
       1004 FORMAT(21H-ACTIVITY SEQUENCE  N,1X,7HSIGMA X,1X,8HSIGMA X2,9X,5HN/
           1MIN,5X,2HAV,10X,2HSS,10X,3HVAR,9X,2HSD,9X,4HVARM,9X,2HSE)
            #RITE(6,1005)
       1005 FORMAT(37H0TIMES FOR UP SORTED BY NEXT ACTIVITY/)
            CALL PSTATS(U,TUU,NUU,RTUU,AVUU)
            CALL PSTATS(R,TUR,NUR,RTUR,AVUR)
            CALL PSTATS(P,TUP,NUP,RTUP,AVUP)
            CALL PSTATS(PSU,TUPSU,NUPSU,RTUPSU,AVUPSU)
            CALL PSTATS(PSM,TUPSM,NUPSM,RTUPSM,AVUPSM)
            CALL PSTATS(PA,TUPA,NUPA,RTUPA,AVUPA)
            CALL PSTATS(PW,TUPW,NUPW,RTUPW,AVUPW)
            CALL PSTATS(PR,TUPR,NUPR,RTUPR,AVUPR)
            CALL PSTATS(PWE,TUPWE,NUPWE,RTUPWE,AVUPWE)
            CALL PSTATS(PAB,TUPAB,NUPAB,RTUPAB,AVUPAB)
            CALL PSTATS(ALL,TU,NU,RTU,AVU)
            WRITE(6,1006)
       1006 FORMAT(39H0TIMES FOR DOWN SORTED BY NEXT ACTIVITY/)
            CALL PSTATS(U,TDU,NDU,RTDU,AVDU)
            CALL PSTATS(R,TDR,NDR,RTDR,AVDR)
            CALL PSTATS(P,TDP,NDP,RTDP,AVDP)
            CALL PSTATS(PSU,TDPSU,NDPSU,RTDPSU,AVDPSU)
            CALL PSTATS(PSM,TDPSM,NDPSM,RTDPSM,AVDPSM)
            CALL PSTATS(PA,TDPA,NDPA,RTDPA,AVDPA)
            CALL PSTATS(PW,TDPW,NDPW,RTDPW,AVDPW)
            CALL PSTATS(PR,TDPR,NDPR,RTDPR,AVDPR)
            CALL PSTATS(PWE,TDPWE,NDPWE,RTDPWE,AVDPWE)
            CALL PSTATS(PAB,TDPAB,NDPAB,RTDPAB,AVDPAB)
            CALL PSTATS(ALL,TD,ND,RTD,AVD)
            WRITE(6,1007)
       1007 FORMAT(38H0TIMES FOR RUN SORTED BY NEXT ACTIVITY/)
            CALL PSTATS(U,TRU,NRU,RTRU,AVRU)
            CALL PSTATS(D,TRD,NRD,RTRD,AVRD)
            CALL PSTATS(P,TRP,NRP,RTRP,AVRP)
            CALL PSTATS(PSU,TRPSU,NRPSU,RTRPSU,AVRPSU)
            CALL PSTATS(PSM,TRPSM,NRPSM,RTRPSM,AVRPSM)
            CALL PSTATS(PA,TRPA,NRPA,RTRPA,AVRPA)
            CALL PSTATS(PW,TRPW,NRPW,RTRPW,AVRPW)
            CALL PSTATS(PR,TRPR,NRPR,RTRPR,AVRPR)
            CALL PSTATS(PWE,TRPWE,NRPWE,RTRPWE,AVRPWE)
            CALL PSTATS(PAB,TRPAB,NRPAB,RTRPAB,AVRPAB)
            CALL PSTATS(ALL,TR,NR,RTR,AVR)
            WRITE(6,1008)
       1008 FORMAT(27H0PECKING AND HANDLING TIMES/)
            CALL PSTATS(P,TP,NP,RTP,AVP)
            CALL PSTATS(PSU,TPSU,NPSU,RTPSU,AVPSU)
            CALL PSTATS(PSM,TPSM,NPSM,RTPSM,AVPSM)
            CALL PSTATS(PA,TPA,NPA,RTPA,AVPA)
            CALL PSTATS(PW,TPW,NPW,RTPW,AVPW)
            CALL PSTATS(PR0,TPR0,NPR0,RTPR0,AVPR0)
            CALL PSTATS(PR1,TPR1,NPR1,RTPR1,AVPR1)
            CALL PSTATS(PR2,TPR2,NPR2,RTPR2,AVPR2)
            CALL PSTATS(PR3,TPR3,NPR3,RTPR3,AVPR3)
            CALL PSTATS(PR4,TPR4,NPR4,RTPR4,AVPR4)
            CALL PSTATS(PR5,TPR5,NPR5,RTPR5,AVPR5)
            CALL PSTATS(PR6,TPR6,NPR6,RTPR6,AVPR6)
            CALL PSTATS(PR7,TPR7,NPR7,RTPR7,AVPR7)
            CALL PSTATS(PR8,TPR8,NPR8,RTPR8,AVPR8)
            CALL PSTATS(PR9,TPR9,NPR9,RTPR9,AVPR9)


            CALL PSTATS(PWE,TPWE,NPWE,RTPWE,AVPWE)
            CALL PSTATS(PAB,TPAB,NPAB,RTPAB,AVPAB)
            WRITE(6,1009)
       1009 FORMAT(40H0TIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK/)
            CALL PSTATS(P,TPU,NPU,RTPU,AVPU)
            CALL PSTATS(PSU,TPSUU,NPSUU,RTPSUU,AVPSUU)
            CALL PSTATS(PSM,TPSMU,NPSMU,RTPSMU,AVPSMU)
            CALL PSTATS(PA,TPAU,NPAU,RTPAU,AVPAU)
            CALL PSTATS(PW,TPWU,NPWU,RTPWU,AVPWU)
            CALL PSTATS(PRA,TPRAU,NPRAU,RTPRAU,AVPRAU)
            CALL PSTATS(PRB,TPRBU,NPRBU,RTPRBU,AVPRBU)
            CALL PSTATS(PRC,TPRCU,NPRCU,RTPRCU,AVPRCU)
            CALL PSTATS(PWE,TPWEU,NPWEU,RTPWEU,AVPWEU)
            CALL PSTATS(PAB,TPABU,NPABU,RTPABU,AVPABU)
            WRITE(6,1010)
       1010 FORMAT(50H0TIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK/)
            CALL PSTATS(P,TPD,NPD,RTPD,AVPD)
            CALL PSTATS(PSU,TPSUD,NPSUD,RTPSUD,AVPSUD)
            CALL PSTATS(PSM,TPSMD,NPSMD,RTPSMD,AVPSMD)
            CALL PSTATS(PA,TPAD,NPAD,RTPAD,AVPAD)
            CALL PSTATS(PW,TPWD,NPWD,RTPWD,AVPWD)
            CALL PSTATS(PRA,TPRAD,NPRAD,RTPRAD,AVPRAD)
            CALL PSTATS(PRB,TPRBD,NPRBD,RTPRBD,AVPRBD)
            CALL PSTATS(PRC,TPRCD,NPRCD,RTPRCD,AVPRCD)
            CALL PSTATS(PWE,TPWED,NPWED,RTPWED,AVPWED)
            CALL PSTATS(PAB,TPABD,NPABD,RTPABD,AVPABD)
            WRITE(6,1011)
       1011 FORMAT(49H0TIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK/)
            CALL PSTATS(P,TPR,NPR,RTPR,AVPR)
            CALL PSTATS(PSU,TPSUR,NPSUR,RTPSUR,AVPSUR)
            CALL PSTATS(PSM,TPSMR,NPSMR,RTPSMR,AVPSMR)
            CALL PSTATS(PA,TPAR,NPAR,RTPAR,AVPAR)
            CALL PSTATS(PW,TPWR,NPWR,RTPWR,AVPWR)
            CALL PSTATS(PRA,TPRAR,NPRAR,RTPRAR,AVPRAR)
            CALL PSTATS(PRB,TPRBR,NPRBR,RTPRBR,AVPRBR)
            CALL PSTATS(PRC,TPRCR,NPRCR,RTPRCR,AVPRCR)
            CALL PSTATS(PWE,TPWER,NPWER,RTPWER,AVPWER)
            CALL PSTATS(PAB,TPABR,NPABR,RTPABR,AVPABR)
      C
      C
      C       OUTPUT FOR FILE STORAGE
      C
      C
            IF(MEDIUM.NE.5)GOTO 6001
       6000 READ(5,6003)NDROP,NPE,NDRI,NU,ND,NR,NP,NPSU,NPSM,NPA,NPW,NPR0,NPR1
           1,NPR2,NPR3,NPR4,NPR5,NPR6,NPR7,NPR8,NPR9,NPWE,NPAB
       6003 FORMAT(6X,2313)
            NPRT=NPR0+NPR1+NPR2+NPR3+NPR4+NPR5+NPR6+NPR7+NPR8+NPR9
            NPTOT=NP+NPSU+NPSM+NPA+NPW+NPRT+NPWE
            REALFT=ZTT
            REALFT=ZFT
            NCARD=NCASE
            RTU=AVU=RTD=AVD=0
            RTR=AVR=RTP=AVP=0
            RTPSU=AVPSU=RTPSM=AVPSM=RTPA=AVPA=RTPW=AVPW=0
            RTPR0=AVPR0=RTPR1=AVPR1=RTPR2=AVPR2=RTPR3=AVPR3=0
            RTPR4=AVPR4=RTPR5=AVPR5=RTPR6=AVPR6=RTPR7=AVPR7=0
            RTPR8=AVPR8=RTPR9=AVPR9=RTPWE=AVPWE=RTPAB=AVPAB=0
            RTUD=AVUD=RTUR=AVUR=RTUP=AVUP=RTUPSU=AVUPSU=0
            RTUPSM=AVUPSM=RTUPA=AVUPA=RTUPW=AVUPW=RTUPR=AVUPR=0
```

```
      RTUPWE=AVUPWE=RTUPAB=AVUPAB=0
      RTRU=AVRU=RTRD=AVRD=RTRP=AVRP=RTRPSU=AVRPSU=0
      RTRPSM=AVRPSM=RTRPA=AVRPA=RTRPW=AVRPW=RTRPR=AVRPR=0
      RTRPWE=AVRPWE=RTRPAB=AVRPAB=0
      RTPU=AVPU=RTPSUU=AVPSUU=RTPSMU=AVPSMU=RTPAU=AVPAU=0
      RTPWU=AVPWU=RTPRAU=AVPRAU=RTPRBU=AVPRBU=RTPRCU=AVPRCU=0
      RTPWEU=AVPWEU=RTPABU=AVPABU=RTPR=AVPR=RTPSUR=AVPSUR=0
      RTPSMR=AVPSMR=RTPAR=AVPAR=RTPWR=AVPWR=RTPRAR=AVPRAR=0
      RTPRBR=AVPRBR=RTPRCR=AVPRCR=RTPWER=AVPWER=RTPABR=AVPABR=0
C
C
C     CHANGE REAL VALUES TO APPARENT INTEGER FOR FILE OUTPUT
C
 6001 JAIR=IFIX(AIRT)
      JMUDT=IFIX(AMUDT)
      JT1=IFIX(HT1)
      JT2=IFIX(HT2)
C
C
      NSER=1
      WRITE(7,19)NCASE,NSER,NC,MEDIUM,MSP,NSEX,NAGE,NDAYS,NFOOT,NDIST,ND
     1IST2,NFLOCK,NPOS,LOC,NSTAT,NTIM,NDATE,NRAIN,NCLOUD,NWIND,NDIR,JAIR
     2,JMUDT,HW1,JT1,HW2,JT2,INDIV,NEARSP,NWET
   19 FORMAT(14,12,12,4I1,12,11,313,11,12,11,14,16,11,11,12,11,13,13,14,
     1I3,14,13,14,12,11)
      NSER=71
      WRITE(7,2001)NCARD,NSER,REALTT,REALFT,NDROP,NPE,NDRI,NPRT,NPTOT
 2001 FORMAT(14,12,2F6.1,312,213)
      NSER=72
      WRITE(7,2000)NCARD,NSER,NUD,RTUD,AVUD,NUR,RTUR,AVUR,NUP,RTUP,AVUP,
     1NUPSU,RTUPSU,AVUPSU
      NSER=73
      WRITE(7,2000)NCARD,NSER,NUPSM,RTUPSM,AVUPSM,NUPA,RTUPA,AVUPA,NUPW,
     1RTUPW,AVUPW,NUPR,RTUPR,AVUPR
      NSER=74
      WRITE(7,2000)NCARD,NSER,NUPWE,RTUPWE,AVUPWE,NUPAB,RTUPAB,AVUPAB,NU
     1,RTU,AVU,ND,RTD,AVD
      NSER=75
      WRITE(7,2000)NCARD,NSER,NRU,RTRU,AVRU,NRD,RTRD,AVRD,NRP,RTRP,AVRP,
     1NRPSU,RTRPSU,AVRPSU
      NSER=76
      WRITE(7,2000)NCARD,NSER,NRPSM,RTRPSM,AVRPSM,NRPA,RTRPA,AVRPA,NRPW,
     1RTRPW,AVRPW,NRPR,RTRPR,AVRPR
      NSER=77
      WRITE(7,2000)NCARD,NSER,NRPWE,RTRPWE,AVRPWE,NRPAB,RTRPAB,AVRPAB,NR
     1,RTR,AVR,NP,RTP,AVP
      NSER=78
      WRITE(7,2000)NCARD,NSER,NPSU,RTPSU,AVPSU,NPSM,RTPSM,AVPSM,NPA,RTPA
     1,AVPA,NPW,RTPW,AVPW
      NSER=79
      WRITE(7,2000)NCARD,NSER,NPR0,RTPR0,AVPR0,NPR1,RTPR1,AVPR1,NPR2,RTP
     1R2,AVPR2,NPR3,RTPR3,AVPR3
      NSER=80
      WRITE(7,2000)NCARD,NSER,NPR4,RTPR4,AVPR4,NPR5,RTPR5,AVPR5,NPR6,RTP
     1R6,AVPR6,NPR7,RTPR7,AVPR7
      NSER=81
      WRITE(7,2000)NCARD,NSER,NPR8,RTPR8,AVPR8,NPR9,RTPR9,AVPR9,NPWE,RTP
     1WE,AVPWE,NPAB,RTPAB,AVPAB
      NSER=82
      WRITE(7,2000)NCARD,NSER,NPU,RTPU,AVPU,NPSUU,RTPSUU,AVPSUU,NPSMU,RT
     1PSMU,AVPSMU,NPAU,RTPAU,AVPAU
      NSER=83
      WRITE(7,2000)NCARD,NSER,NPWU,RTPWU,AVPWU,NPRAU,RTPRAU,AVPRAU,NPRBU
     1,RTPRBU,AVPRBU,NPRCU,RTPRCU,AVPRCU
      NSER=84
      WRITE(7,2000)NCARD,NSER,NPWEU,RTPWEU,AVPWEU,NPABU,RTPABU,AVPABU,NP
     1R,RTPR,AVPR,NPSUR,RTPSUR,AVPSUR
      NSER=85
      WRITE(7,2000)NCARD,NSER,NPSMR,RTPSMR,AVPSMR,NPAR,RTPAR,AVPAR,NPWR,
     1RTPWR,AVPWR,NPRAR,RTPRAR,AVPRAR
      NSER=86
      WRITE(7,2000)NCARD,NSER,NPRBR,RTPRBR,AVPRBR,NPRCR,RTPRCR,AVPRCR,NP
     1WER,RTPWER,AVPWER,NPABR,RTPABR,AVPABR
 2000 FORMAT(14,12,4(13,F6.2,F9.3))
      GOTO 1
      END
C
C
C
      SUBROUTINE PSTATS(ITEM,A,N,SSUMA,SSUMA2)
      COMMON FEEDT
      DIMENSION A(20)
      REAL*8 SUMA,SUMA2,SSA
      T=FEEDT/600.
C
C     SET ZEROS
C
      SUMA=0
      SUMA2=0
      SSUMA=0
      SSUMA2=0
C
C     LOOP FOR SUM AND SUM OF SQUARES
C
      IF(N.LT.1)GOTO 15
      DO 10 I=1,N
      SUMA=SUMA+A(I)/10
      SUMA2=SUMA2+A(I)*A(I)/100
   10 CONTINUE
C
C     CALCULATE
C
      SSUMA=SUMA
      SSUMA2=SUMA2
      AVA=SUMA/FLOAT(N)
      SSA=SUMA2-SUMA*SUMA/FLOAT(N)
      IF(N.EQ.1)GOTO 21
      VARA=SSA/(FLOAT(N)-1)
      IF(VARA.LE.0)VARA=0
      GOTO 20
   21 VARA=0.
      GOTO 20
   20 SDA=SQRT(VARA)
      VARMA=VARA/FLOAT(N)
      IF(VARMA.LE.0)VARMA=0
      SEA=SQRT(VARMA)
      IF(FEEDT.EQ.0)GOTO 16
      RATN=FLOAT(N)/T
C
C     PRINT RESULT
```

```
 1081      C
 1082        17 WRITE(6,100)ITEM,N,SSUMA,SSUMA2,RATN,AVA,SSA,VARA,SDA,VARMA,SEA
 1083       100 FORMAT(1H ,A4,10X,I3,F6.1,8F12.3)
 1084           RETURN
 1085        15 WRITE(6,101)ITEM
 1086       101 FORMAT(1H ,A4,8X,4HZERO)
 1087           RETURN
 1088        16 RATN=-0
 1089           GOTO 17
 1090           END
 1091      $DATA
 1092      $STOP
END OF FILE
```

SECTION 3. LISTING OF 'PLOVP2'

```
      $COMPILE
      C
      C                                  PLOVP2
      C                                  ======
      C
      C     AUTHOR: M W PIENKOWSKI     PROGRAM MODIFIED FROM "PLOVPROG" APRIL 1979
      C     THIS LISTING INCORPORATES MODIFICATIONS UP TO SEPTEMBER 1979
      C
      C     A MODIFICATION OF "PLOVPROG" FOR TIME-BASED DATA ONLY. TIMES SPENT
      C     RUNNING ARE ABSORBED INTO PRECEDING OR FOLLOWING PECK-TYPE ACTIVITIES
      C     IF SUCH ACTIVITY IS ADJACENT. FOLLOWING PECKS TAKE PRECEDENCE OVER
      C     PRECEDING. IF NO SUCH PECK-TYPE ACTIVITY IS ADJACENT, RUN IS RETAINED.
      C     REARRANGED DATA ARE THEN PRINTED (ON LOGICAL UNIT 6) AND USED AS THE
      C     INPUT TO "PLOVPROG" TYPE ANALYSIS, RESULTING IN PRINT-OUT OF BASIC
      C     STATISTICS FOR EACH CASE AND WRITING TO FILE OF SORTED DATA FOR
      C     EACH CASE.
      C
      C     THE PROGRAM IS WRITTEN IN FORTRAN IV LANGUAGE AS ACCEPTED BY THE
      C     COMPILER *WATFIV; SLIGHT MODIFICATION WOULD BE NECESSARY FOR USE
      C     WITH OTHER FORTRAN COMPILERS. CARDS (OR CARD IMAGES) ARE READ ON
      C     LOGICAL UNIT 5; BASIC CASE STATISTICS ARE PRINTED ON LOGICAL UNIT
      C     6; AND SORTED DATA ARE OUTPUT ON LOGICAL UNIT 7.
      C
      C
            DIMENSION NACT(500),T(500),TUD(99),TUR(99),          TUPSU(99),TUPSM
           1(99),TUPA(99),TUPW(99),TUPR(99),TDU(99),TDR(99),TDPSU(99),TDPSM(99
           2),TDPA(99),TDPW(99),TDPR(99),TRU(99),TRD(99),TRP(99),TRPSU(99),TRP
           3SM(99),TRPA(99),TRPW(99),TRPR(99),          TPSU(99),TPSM(99),TPA(99)
           4,TPW(99),TPR0(99),TPR1(99),TPR2(99),TPR3(99),TPR4(99),TPR5(99),TPR
           56(99),TPR7(99),TPR8(99),TPR9(99),          TPD(99),          TPSUU(99)
           6,TPSUD(99),TPSUR(99),TPSMU(99),TPSMD(99),TPSMR(99),TPAU(99),TPAD(9
           79),TPAR(99),TPWU(99),TPWD(99),TPWR(99),TPRAU(99),TPRAD(99),TPRAR(9
           89),TPR0U(99),TPR0D(99),TPR0R(99),TPRCU(99),TPRCD(99),TPRCR(99)
            DIMENSION TP(200),TPU(200),TPR(200),TUP(300)
            DIMENSION TUPWE(99),TUPAB(99),TDPWE(99),TDPAR(99),TRPWE(99),TRPAB(
           199),TPAB(99),TPABU(99),TPABD(99),TPABR(99),TPWE(99),TPWEU(99),TPWE
           2D(99),TPWER(99)
            DIMENSION TDP(99)
            DIMENSION TU(500),TD(500),TR(500)
            DIMENSION NAC2(500),T2(500)
            COMMON FEEDF
            REAL MT1,MT2
            INTEGER HW1,HW2
            INTEGER ALL
            INTEGER PRA,PRB,PRC
            INTEGER U,D,R,OR,SP,SB,SR,SS,P,PSU,PSM,PA,PW,PR0,PR1,PR2,PR3,PR4,P
           1R5,PR6,PR7,PR8,PR9
            INTEGER PAB,PWE,PE,TN,SI,SD,DRI
            INTEGER PR
            INTEGER STOP
            DATA STOP/4HSTOP/
            DATA U,D,R,DR,SP,SB,SR,SS,P,PSU,PSM,PA,PW,PR,PRA,PRB,PRC,PR1,PR2,P
           1R3,PR4,PR5,PR6,PR7,PR8,PR9/1HU,1HD,1HR,2HDR,2HSP,2HSB,2HSR,2HSS,1H
           2P,3HPSU,3HPSM,2HPA,2HPW,2HPR,3HPRA,3HPRB,3HPRC,3HPR1,3HPR2,3HPR3,3
           3HPR4,3HPR5,3HPR6,3HPR7,3HPR8,3HPR9/
            DATA PWE,PAB,PE,SI,SD,DRI/3HPWE,3HPAB,2HPE,2HSI,2HSD,3HDRI/
            DATA PR0/3HPR0/
            DATA TN/2HTN/
            DATA ALL/3HALL/
            DATA MCD,MCT,MTD,MTT,M,MF,MN,MNE,ME,MSE,MS,MSW,MW,MNW/4HC/DI,4HC/T
```

```
     1,4HT/01,4HT/TI,1HM,1HF,1HN,2HNE,1HE,2HSE,1HS,2HSW,1HW,2HNW/
      DATA MTN/4HT/NO/
C
C
C       INPUT DATA
C
C
      1 READ(5,101)NCASE,NSER,NC,MEDIUM,MSP,NSEX,NAGE,NDAYS,NFOOT,NDIST,ND
     1IST2,NFLOCK,NPOS,LOC,NSTAT,NTIM,NDATE,NRAIN,NCLOUD,NWIND,NDIR,AIRT
     2,AMUDT,HW1,HT1,HW2,HT2,INDIV,NEARSP,NWET,ZTT,ZFT
       IF(NCASE.EQ.-109)STOP
       IF(MEDIUM.EQ.5)GOTO 3010
       DO 10 I=1,NC
       NL=9*I-8
       NH=9*I
   10 READ(5,100)(NAC2(J),T2(J),J=NL,NH)
  101 FORMAT(14,12,12,411,12,11,313,11,12,11,14,16,11,11,12,11,F3.0,F3.0
     1,14,F3.0,14,F3.0,14,12,11,2F4.0)
  100 FORMAT(8X,9(A4,F4.0))
       IF(MEDIUM.EQ.1)MMED=MTT
       IF(MEDIUM.EQ.2)MMED=MTD
       IF(MEDIUM.EQ.3)MMED=MCT
       IF(MEDIUM.EQ.4)MMED=MCO
       IF(MEDIUM.EQ.5)MMED=MTN
       MC=NC+1
       NCARD=NCASE
       WRITE(6,3000)NCASE,MC,MMED
 3000 FORMAT(1H1,9HCASE NO. ,I4,3H , ,I2,23H INITIAL DATA CARDS.   ,A4,1
     10X,'RUNS INCLUDED IN PECK-TIME')
       IF(MSP.EQ.1)GOTO 3001
       IF(MSP.EQ.2)GOTO 3002
       IF(MSP.EQ.3)GOTO 3011
       IF(MSP.EQ.4)GOTO 3013
       IF(MSP.EQ.5)GOTO 3016
       IF(MSP.EQ.6)GOTO 3017
       WRITE(6,3020)MSP
 3020 FORMAT(12HOSPECIES NO.,I4)
 3001 WRITE(6,3003)
 3003 FORMAT(14HORINGED PLOVER)
       GOTO 3004
 3002 WRITE(6,3005)
 3005 FORMAT(12HOGREY PLOVER)
       GOTO 3004
 3011 WRITE(6,3012)
 3012 FORMAT(7HODUNLIN)
       GOTO 3004
 3016 WRITE(6,3018)
 3018 FORMAT(14HOGOLDEN PLOVER)
       GOTO 3004
 3017 WRITE(6,3019)
 3019 FORMAT(8HOLAPWING)
       GOTO 3004
 3013 WRITE(6,3014)
 3014 FORMAT(11HOSANDERLING)
 3004 CONTINUE
       WRITE(6,4000)INDIV
 4000 FORMAT(15H INDIVIDUAL NO.,I4)
       RAIRT=AIRT/10
       RAMUDT=AMUDT/10
       MT1=HT1/10


       MT2=HT2/10
       IF(NSEX.EQ.0)NSEX=0
       IF(NSEX.EQ.1)NSEX=M
       IF(NSEX.EQ.2)NSEX=MF
       WRITE(6,3006)NSEX,NAGE,NDAYS,NSTAT,LOC,NTIM,NDATE
 3006 FORMAT(4H SEX,A4,12H,  AGE CODE ,I1,12H (CHICK AGE ,I2,16H DAYS),
     1STATUS: ,I1,17H, LOCATION CODE: ,I2,8H, TIME: ,I4,8H, DATE: ,I6)
       IF(NDIR.EQ.0)MDIR=0
       IF(NDIR.EQ.1)MDIR=MN
       IF(NDIR.EQ.2)MDIR=MNE
       IF(NDIR.EQ.3)MDIR=ME
       IF(NDIR.EQ.4)MDIR=MSE
       IF(NDIR.EQ.5)MDIR=MS
       IF(NDIR.EQ.6)MDIR=MSW
       IF(NDIR.EQ.7)MDIR=MW
       IF(NDIR.EQ.8)MDIR=MNW
       WRITE(6,3007)NRAIN,NCLOUD,NWIND,MDIR,RAIRT,RAMUDT,HW1,MT1,HW2,MT2
 3007 FORMAT(12HORAIN CODE: ,I1,9H, CLOUD: ,I1,16H/8, WIND FORCE: ,I2,6H
     1 FROM ,A4,12H, AIR TEMP: ,F4.1,18H, SUBSTRATE TEMP: ,F4.1,8H, HW A
     2T ,I4,3H ( ,F4.1,7H ) AND ,I4,3H ( ,F4.1,2H ))
       WRITE(6,3008)NFOOT,NDIST,NDIST2,NFLOCK,NPOS
 3008 FORMAT(1H ,11HFOOTSHAKE: ,I1,33H, DISTANCE FROM NEAREST SAME SP: ,
     1I3,14H M, OTHER SP: ,I3,16H M, FLOCK SIZE: ,I3,21H, POSITION IN FL
     2OCK: ,I1)
       IF(INDIV.EQ.0)GOTO 3010
       WRITE(6,3009)INDIV
 3009 FORMAT(21H0INDIVIDUAL CODE NO. ,I4)
 3010 CONTINUE
C
C
C       SET  ZEROS
C
C
       NDROP=0
       NUPWE=NUPAB=NDPWE=NDPAB=NRPWE=NRPAB=NPE=NSI=NSD=NPAB=NPABU=0
       NPABD=NPABR=NPWE=NPWEU=NPWED=NPWER=NDRI=NPU=NPD=NPR=NPSUU=0
       NPSUD=NPSUR=NPSMU=NPSMD=NPSMR=NPAU=NPAD=NPAR=NPWU=NPWD=NPWR=0
       NPRAJ=NPRAD=NPRAR=NPRBU=NPRBD=NPRBR=NPRCU=NPRCD=NPRCR=0
       NU=ND=NR=NDR=NSP=NSB=NSR=NSS=NP=NPSU=NPSM=NPA=NPW=NPR0=NPR1=0
       NPR2=NPR3=NPR4=NPR5=NPR6=NPR7=NPR8=NPR9=NPRT=0
       TOTT=FEEDT=0.
       NUD=NUR=NUP=NUPSU=NUPSM=NUPA=NUPW=NUPR=NDU=NDR=NDPSU=NDPSM=0
       NDP=0
       NDPA=NDPW=NDPR=NRU=NRD=NRP=NRPSU=NRPSM=NRPA=NRPW=NRPR=0
       IF(MEDIUM.EQ.5)GOTO 6000
C
C
C       RECODING TO COMBINE RUNS WITH PECKS
C
C
       I=1
       J=1
 7002  IF(NAC2(I).EQ.STOP)GOTO 7005
       IF(NAC2(I).EQ.TN)NAC2(I)=R
       IF(NAC2(I).NE.R)GOTO 7000
 7001  IF(NAC2(I+1).NE.U.AND.NAC2(I+1).NE.D.AND.NAC2(I+1).NE.DR.AND.NAC2(
     1I+1).NE.PE.AND.NAC2(I+1).NE.SP.AND.NAC2(I+1).NE.SB.AND.NAC2(I+1).N
     2E.SR.AND.NAC2(I+1).NE.SS.AND.NAC2(I+1).NE.SI.AND.NAC2(I+1).NE.SD.A
     3ND.NAC2(I+1).NE.STOP.AND.NAC2(I+1).NE.R)GOTO 7004
       IF(I.EQ.1)GOTO 7000
```

```
      IF(NAC2(I-1).NE.U.AND.NAC2(I-1).NE.D.AND.NAC2(I-1).NE.DR.AND.NAC2(
     1I-1).NE.PE.AND.NAC2(I-1).NE.SP.AND.NAC2(I-1).NE.SB.AND.NAC2(I-1).N
     2E.SR.AND.NAC2(I-1).NE.SS.AND.NAC2(I-1).NE.SI.AND.NAC2(I-1).NE.SD.A
     3ND.NAC2(I-1).NE.R)GOTO 7003
      GOTO 7000
7004  T2(I+1)=T2(I+1)+T2(I)
      I=I+1
      GOTO 7002
7003  T(J-1)=T(J-1)+T2(I)
      I=I+1
      GOTO 7002
7000  NACT(J)=NAC2(I)
      T(J)=T2(I)
      I=I+1
      J=J+1
      GOTO 7002
7005  NACT(J)=NAC2(I)
      T(J)=0
      WRITE(6,7006)
      WRITE(6,7007)(NACT(I),T(I),I=1,J)
7006  FORMAT('0RECODED DATA:')
7007  FORMAT(' ',9(A4,F5.0,4X))
C
C
C       SORT FIRST ACTIVITIES
C
C
      I=1
      GOTO 76
   74 FEEDT=FEEDT+T(I)
   78 TOTT=TOTT+T(I)
   77 I=I+1
   76 IF(NACT(I).EQ.U)GOTO 50
      IF(NACT(I).EQ.D)GOTO 51
      IF(NACT(I).EQ.TN)NACT(I)=R
      IF(NACT(I).EQ.R)GOTO 52
      IF(NACT(I).EQ.DR)GOTO 53
      IF(NACT(I).EQ.PE)GOTO 81
      IF(NACT(I).EQ.SP)GOTO 54
      IF(NACT(I).EQ.SB)GOTO 55
      IF(NACT(I).EQ.SR)GOTO 56
      IF(NACT(I).EQ.SS)GOTO 57
      IF(NACT(I).EQ.SI)GOTO 79
      IF(NACT(I).EQ.SD)GOTO 80
      IF(NACT(I).EQ.P)GOTO 58
      IF(NACT(I).EQ.PSU)GOTO 59
      IF(NACT(I).EQ.PSM)GOTO 60
      IF(NACT(I).EQ.PA)GOTO 61
      IF(NACT(I).EQ.PW)GOTO 62
      IF(NACT(I).EQ.PR0)GOTO 63
      IF(NACT(I).EQ.PR1)GOTO 64
      IF(NACT(I).EQ.PR2)GOTO 65
      IF(NACT(I).EQ.PR3)GOTO 66
      IF(NACT(I).EQ.PR4)GOTO 67
      IF(NACT(I).EQ.PR5)GOTO 68
      IF(NACT(I).EQ.PR6)GOTO 69
      IF(NACT(I).EQ.PR7)GOTO 70
      IF(NACT(I).EQ.PR8)GOTO 71
      IF(NACT(I).EQ.PR9)GOTO 72
      IF(NACT(I).EQ.PAB)GOTO 82


      IF(NACT(I).EQ.PWE)GOTO 83
      IF(NACT(I).EQ.DRI)GOTO 84
      IF(NACT(I).EQ.STOP)GOTO 75
C
C       ( GO TO CALCULATE AND PRINT OUT )
C
      WRITE(6,201)I
  201 FORMAT(31HOUNRECOGNISED CODE AT ACTIVITY ,I4)
      GOTO 1
C
C       ( GO TO NEXT CASE )
C
C
C
C       FIRST ACTIVITY = U
C
C
   50 NU=NU+1
      K=0
      IF(NACT(I+1).NE.OR)GOTO 501
      K=1
      T(I)=T(I)+T(I+1)
  501 L=I+1+K
      TU(NU)=T(I)
      IF(NACT(L).EQ.D)GOTO 502
      IF(NACT(L).EQ.R.OR.NACT(L).EQ.TN)GOTO 503
      IF(NACT(L).EQ.P)GOTO 504
      IF(NACT(L).EQ.PSU)GOTO 505
      IF(NACT(L).EQ.PSM)GOTO 506
      IF(NACT(L).EQ.PA)GOTO 507
      IF(NACT(L).EQ.PW)GOTO 508
      IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
     1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
     2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 509
      IF(NACT(L).EQ.PWE)GOTO 500
      IF(NACT(L).EQ.PAB)GOTO 5000
      GOTO 74
  502 NUD=NUD+1
      TUD(NUD)=T(I)
      GOTO 74
  503 NUR=NUR+1
      TUR(NUR)=T(I)
      GOTO 74
  504 NUP=NUP+1
      TUP(NUP)=T(I)
      GOTO 74
  505 NUPSU=NUPSU+1
      TUPSU(NUPSU)=T(I)
      GOTO 74
  506 NUPSM=NUPSM+1
      TUPSM(NUPSM)=T(I)
      GOTO 74
  507 NUPA=NUPA+1
      TUPA(NUPA)=T(I)
      GOTO 74
  508 NUPW=NUPW+1
      TUPW(NUPW)=T(I)
      GOTO 74
  509 NUPR=NUPR+1
      TUPR(NUPR)=T(I)
```

```
      GOTO 74
  500 NUPWE=NUPWE+1
      TUPWE(NUPWE)=T(I)
      GOTO 74
 5000 NUPAB=NUPAB+1
      TUPAB(NUPAB)=T(I)
      GOTO 74
C
C
C       FIRST ACTIVITY = D  (DOWN)
C
C
   51 ND=ND+1
      K=0
      IF(NACT(I+1).NE.OR)GOTO 511
      K=1
      T(I)=T(I)+T(I+1)
  511 L=I+1+K
      TD(ND)=T(I)
      IF(NACT(L).EQ.U)GOTO 512
      IF(NACT(L).EQ.R.OR.NACT(L).EQ.TN)GOTO 513
      IF(NACT(L).EQ.P)GOTO 514
      IF(NACT(L).EQ.PSU)GOTO 515
      IF(NACT(L).EQ.PSM)GOTO 516
      IF(NACT(L).EQ.PA)GOTO 517
      IF(NACT(L).EQ.PW)GOTO 518
      IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
     1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
     2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 519
      IF(NACT(L).EQ.PWE)GOTO 510
      IF(NACT(L).EQ.PAB)GOTO 5100
      GOTO 74
  512 NDU=NDU+1
      TDU(NDU)=T(I)
      GOTO 74
  513 NDR=NDR+1
      TDR(NDR)=T(I)
      GOTO 74
  514 NDP=NDP+1
      TDP(NDP)=T(I)
      GOTO 74
  515 NDPSU=NDPSU+1
      TDPSU(NDPSU)=T(I)
      GOTO 74
  516 NDPSM=NDPSM+1
      TDPSM(NDPSM)=T(I)
      GOTO 74
  517 NDPA=NDPA+1
      TDPA(NDPA)=T(I)
      GOTO 74
  518 NDPW=NDPW+1
      TDPW(NDPW)=T(I)
      GOTO 74
  519 NDPR=NDPR+1
      TDPR(NDPR)=T(I)
      GOTO 74
  510 NDPWE=NDPWE+1
      TDPWE(NDPWE)=T(I)
      GOTO 74
 5100 NDPAB=NDPAB+1
      TDPAB(NDPAB)=T(I)
      GOTO 74
C
C
C       FIRST ACTIVITY = R ( OR T )        (RUN - OR TURN)
C
C
   52 NR=NR+1
      K=0
      IF(NACT(I+1).NE.OR)GOTO 521
      K=1
      T(I)=T(I)+T(I+1)
  521 L=I+1+K
      TR(NR)=T(I)
      IF(NACT(L).EQ.U)GOTO 522
      IF(NACT(L).EQ.D)GOTO 523
      IF(NACT(L).EQ.P)GOTO 524
      IF(NACT(L).EQ.PSU)GOTO 525
      IF(NACT(L).EQ.PSM)GOTO 526
      IF(NACT(L).EQ.PA)GOTO 527
      IF(NACT(L).EQ.PW)GOTO 528
      IF(NACT(L).EQ.PR0.OR.NACT(L).EQ.PR1.OR.NACT(L).EQ.PR2.OR.NACT(L).E
     1Q.PR3.OR.NACT(L).EQ.PR4.OR.NACT(L).EQ.PR5.OR.NACT(L).EQ.PR6.OR.NAC
     2T(L).EQ.PR7.OR.NACT(L).EQ.PR8.OR.NACT(L).EQ.PR9)GOTO 529
      IF(NACT(L).EQ.PWE)GOTO 520
      IF(NACT(L).EQ.PAB)GOTO 5200
      GOTO 74
  522 NRU=NRU+1
      TRU(NRU)=T(I)
      GOTO 74
  523 NRD=NRD+1
      TRD(NRD)=T(I)
      GOTO 74
  524 NRP=NRP+1
      TRP(NRP)=T(I)
      GOTO 74
  525 NRPSU=NRPSU+1
      TRPSU(NRPSU)=T(I)
      GOTO 74
  526 NRPSM=NRPSM+1
      TRPSM(NRPSM)=T(I)
      GOTO 74
  527 NRPA=NRPA+1
      TRPA(NRPA)=T(I)
      GOTO 74
  528 NRPW=NRPW+1
      TRPW(NRPW)=T(I)
      GOTO 74
  529 NRPR=NRPR+1
      TRPR(NRPR)=T(I)
      GOTO 74
  520 NRPWE=NRPWE+1
      TRPWE(NRPWE)=T(I)
      GOTO 74
 5200 NRPAB=NRPAB+1
      TRPAB(NRPAB)=T(I)
      GOTO 74
C
C
C   FIRST ACTIVITY = DR  ( DROPPING )
```

```
C
C
   53 NDROP=NDROP+1
      GOTO 77
C
C
C      FIRST ACTIVITY = PE  ( PELLET )
C
C
   81 NPE=NPE+1
      GOTO 77
C
C
C      FIRST ACTIVITY = SP  ( STOP   PREEN )
C
C
   54 NSP=NSP+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,202)REALT,REALT2
  202 FORMAT(13H PREENING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = SB  ( STOP    BATHE )
C
C
   55 NSB=NSB+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,203)REALT,REALT2
  203 FORMAT(12H BATHING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = SR  ( STOP   ROOSTING )
C
C
   56 NSR=NSR+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,204)REALT,REALT2
  204 FORMAT(13H ROOSTING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = SS  ( STOP    STANDING )
C
C
   57 NSS=NSS+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,205)REALT,REALT2
  205 FORMAT(13H STANDING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = SI  ( STOP    INCUBATE OR BROOD )
C
C
   79 NSI=NSI+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,206)REALT,REALT2
  206 FORMAT(27H INCUBATING OR BROODING AT ,F5.1,14H SECONDS TILL ,F5.1,
     18H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = SD  ( STOP    DISPLAY )
C
C
   80 NSD=NSD+1
      REALT=TOTT/10.
      REALT2=(TOTT+T(I))/10.
      WRITE(6,207)REALT,REALT2
  207 FORMAT(15H DISPLAYING AT ,F5.1,14H SECONDS TILL ,F5.1,8H SECONDS)
      GOTO 78
C
C
C      FIRST ACTIVITY = P  ( PECK )
C
C
   58 NP=NP+1
      TP(NP)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 580
      IF(NACT(I+1).EQ.D)GOTO 581
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 582
      GOTO 74
  580 NPU=NPU+1
      TPU(NPU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPU(NPU)=TPU(NPU)+T(I+2)
      GOTO 74
  581 NPD=NPD+1
      TPD(NPD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPD(NPD)=TPD(NPD)+T(I+2)
      GOTO 74
  582 NPR=NPR+1
      TPR(NPR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPR(NPR)=TPR(NPR)+T(I+2)
      GOTO 74
C
C
C      FIRST ACTIVITY = PSU    (  PECK   SUCCESS )
C
C
   59 NPSU=NPSU+1
      TPSU(NPSU)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 590
      IF(NACT(I+1).EQ.D)GOTO 591
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 592
      GOTO 74
  590 NPSUU=NPSUU+1
      TPSUU(NPSUU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUU(NPSUU)=TPSUU(NPSUU)+T(
     1I+2)
      GOTO 74
  591 NPSUD=NPSUD+1
      TPSUD(NPSUD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUD(NPSUD)=TPSUD(NPSUD)+T(
```

```
     1[+2)
      GOTO 74
  592 NPSUR=NPSUR+1
      TPSUR(NPSUR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSUR(NPSUR)=TPSUR(NPSUR)+T(
     1I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY  =  PSM     (  PECK    SMALL ITEM  )
C
C
   60 NPSM=NPSM+1
      TPSM(NPSM)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 600
      IF(NACT(I+1).EQ.D)GOTO 601
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 602
      GOTO 74
  600 NPSMU=NPSMU+1
      TPSMU(NPSMU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMU(NPSMU)=TPSMU(NPSMU)+T(
     1I+2)
      GOTO 74
  601 NPSMD=NPSMD+1
      TPSMD(NPSMD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMD(NPSMD)=TPSMD(NPSMD)+T(
     1I+2)
  602 NPSMR=NPSMR+1
      TPSMR(NPSMR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPSMR(NPSMR)=TPSMR(NPSMR)+T(
     1I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PA    ( PECK   ARENICOLA )
C
C
C
   61 NPA=NPA+1
      TPA(NPA)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 610
      IF(NACT(I+1).EQ.D)GOTO 611
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 612
      GOTO 74
  610 NPAU=NPAU+1
      TPAU(NPAU)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAU(NPAU)=TPAU(NPAU)+T(I+2)
      GOTO 74
  611 NPAD=NPAD+1
      TPAD(NPAD)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAD(NPAD)=TPAD(NPAD)+T(I+2)
      GOTO 74
  612 NPAR=NPAR+1
      TPAR(NPAR)=T(I)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPAR(NPAR)=TPAR(NPAR)+T(I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PW    ( PECK    WORM - UNIDENTIFIED )
C
C
C
   62 NPW=NPW+1
      TPW(NPW)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 620
      IF(NACT(I+1).EQ.D)GOTO 621
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 622
      GOTO 74
  620 NPWU=NPWU+1
      TPWU(NPWU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWU(NPWU)=TPWU(NPWU)+T(I+2)
      GOTO 74
  621 NPWD=NPWD+1
      TPWD(NPWD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWD(NPWD)=TPWD(NPWD)+T(I+2)
      GOTO 74
  622 NPWR=NPWR+1
      TPWR(NPWR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWR(NPWR)=TPWR(NPWR)+T(I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = PR0-9    ( PECK    RED   WORM )
C
C
C
C       PR0    ( SMALL RED WORM )
C
   63 NPR0=NPR0+1
      TPR0(NPR0)=T(I)
      GOTO 630
C
C       PR1    ( 1/4 RED WORMS )
C
   64 NPR1=NPR1+1
      TPR1(NPR1)=T(I)
      GOTO 630
C
C    SMALL RED WORMS  ( PR0 & PR1 )
C
  630 IF(NACT(I+1).EQ.U)GOTO 631
      IF(NACT(I+1).EQ.D)GOTO 632
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 633
      GOTO 74
  631 NPRAU=NPRAU+1
      TPRAU(NPRAU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAU(NPRAU)=TPRAU(NPRAU)+T(
     1I+2)
      GOTO 74
  632 NPRAD=NPRAD+1
      TPRAD(NPRAD)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAD(NPRAD)=TPRAD(NPRAD)+T(
     1I+2)
      GOTO 74
  633 NPRAR=NPRAR+1
      TPRAR(NPRAR)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAR(NPRAR)=TPRAR(NPRAR)+T(
     1I+2)
      GOTO 74
C
C       PR2    ( 1/2 RED WORMS  )
C
   65 NPR2=NPR2+1
```

```
661             TPR2(NPR2)=T(I)
662             GOTO 650
663       C
664       C       PR3    ( 3/4 RED WORMS  )
665       C
666          66 NPR3=NPR3+1
667             TPR3(NPR3)=T(I)
668             GOTO 650
669       C
670       C       PR4    (  1 RED WORMS  )
671       C
672          67 NPR4=NPR4+1
673             TPR4(NPR4)=T(I)
674             GOTO 650
675       C
676       C       MEDIUM RED WORMS    ( PR2, PR3 & PR4  )
677       C
678         650 IF(NACT(I+1).EQ.U)GOTO 651
679             IF(NACT(I+1).EQ.D)GOTO 652
680             IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 653
681             GOTO 74
682         651 NPRBU=NPRBU+1
683             TPRBU(NPRBU)=T(I+1)
684             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRBU(NPRBU)=TPRBU(NPRBU)+T(
685            (I+2)
686             GOTO 74
687         652 NPRBD=NPRBD+1
688             TPRBD(NPRBD)=T(I+1)
689             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRBD(NPRBD)=TPRBD(NPRBD)+T(
690            (I+2)
691             GOTO 74
692         653 NPRBR=NPRBR+1
693             TPRBR(NPRBR)=T(I+1)
694             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRAR(NPRAR)=TPRAR(NPRAR)+T(
695            (I+2)
696             GOTO 74
697       C
698       C       PR5    ( 1 1/4 RED WORMS  )
699       C
700          68 NPR5=NPR5+1
701             TPR5(NPR5)=T(I)
702             GOTO 680
703       C
704       C       PR6    (  1 1/2 RED WORMS  )
705       C
706          69 NPR6=NPR6+1
707             TPR6(NPR6)=T(I)
708             GOTO 680
709       C
710       C       PR7    (  1 3/4 RED WORMS  )
711       C
712          70 NPR7=NPR7+1
713             TPR7(NPR7)=T(I)
714             GOTO 680
715       C
716       C       PR8    (  2 RED WORMS  )
717       C
718          71 NPR8=NPR8+1
719             TPR8(NPR8)=T(I)
720             GOTO 680


721       C
722       C       PR9    (  >2 RED WORMS  )
723       C
724          72 NPR9=NPR9+1
725             TPR9(NPR9)=T(I)
726             GOTO 680
727       C
728       C       LARGE RED WORMS    ( PR5, PR6, PR7, PR8 & PR9  )
729       C
730         680 IF(NACT(I+1).EQ.U)GOTO 681
731             IF(NACT(I+1).EQ.D)GOTO 682
732             IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 683
733             GOTO 74
734         681 NPRCU=NPRCU+1
735             TPRCU(NPRCU)=T(I+1)
736             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCU(NPRCU)=TPRCU(NPRCU)+T(
737            (I+2)
738             GOTO 74
739         682 NPRCD=NPRCD+1
740             TPRCD(NPRCD)=T(I+1)
741             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCD(NPRCD)=TPRCD(NPRCD)+T(
742            (I+2)
743             GOTO 74
744         683 NPRCR=NPRCR+1
745             TPRCR(NPRCR)=T(I+1)
746             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPRCR(NPRCR)=TPRCR(NPRCR)+T(
747            (I+2)
748             GOTO 74
749       C
750       C
751       C       FIRST ACTIVITY = PAB  ( PECK - ABORTED  )
752       C
753       C
754          82 NPAB=NPAB+1
755             TPAB(NPAB)=T(I)
756             IF(NACT(I+1).EQ.U)GOTO 820
757             IF(NACT(I+1).EQ.D)GOTO 821
758             IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 822
759             GOTO 74
760         820 NPABU=NPABU+1
761             TPABU(NPABU)=T(I+1)
762             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABU(NPABU)=TPABU(NPABU)+T(
763            (I+2)
764             GOTO 74
765         821 NPABD=NPABD+1
766             TPABD(NPABD)=T(I+1)
767             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABD(NPABD)=TPABD(NPABD)+T(
768            (I+2)
769             GOTO 74
770         822 NPABR=NPABR+1
771             TPABR(NPABR)=T(I+1)
772             IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPABR(NPABR)=TPABR(NPABR)+T(
773            (I+2)
774             GOTO 74
775       C
776       C
777       C       FIRST ACTIVITY = PWE   ( PECK - WEED  )
778       C
779       C
780          83 NPWE=NPWE+1
```

```
      TPWE(NPWE)=T(I)
      IF(NACT(I+1).EQ.U)GOTO 830
      IF(NACT(I+1).EQ.D)GOTO 831
      IF(NACT(I+1).EQ.R.OR.NACT(I+1).EQ.TN)GOTO 832
      GOTO 74
  830 NPWEU=NPWEU+1
      TPWEU(NPWEU)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWEU(NPWEU)=TPWEU(NPWEU)+T(
     1I+2)
      GOTO 74
  831 NPWED=NPWED+1
      TPWED(NPWED)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWED(NPWED)=TPWED(NPWED)+T(
     1I+2)
      GOTO 74
  832 NPWER=NPWER+1
      TPWER(NPWER)=T(I+1)
      IF(NACT(I+2).EQ.DR.OR.NACT(I+2).EQ.PE)TPWER(NPWER)=TPWER(NPWER)+T(
     1I+2)
      GOTO 74
C
C
C       FIRST ACTIVITY = DRI    (  DRINK  )
C
C
   84 NDRI=NDRI+1
      GOTO 74
C
C
C       INITIAL TOTALLING CALCULATIONS
C
C
   75 IF(MEDIUM.EQ.2)FEEDT=ZFT*10.
      IF(MEDIUM.EQ.2)TOTT=ZTT*10.
      RATU=FLOAT(NU)/(FEEDT/600.)
      RATD=FLOAT(ND)/(FEEDT/600.)
      RATR=FLOAT(NR)/(FEEDT/600.)
      RATDR1=FLOAT(NDROP)/(FEEDT/600.)
      RATDR2=FLOAT(NDROP)/(TOTT/600.)
      RATPE1=FLOAT(NPE)/(FEEDT/600.)
      RATPE2=FLOAT(NPE)/(TOTT/600.)
      RATP=FLOAT(NP)/(FEEDT/600.)
      RATPSU=FLOAT(NPSU)/(FEEDT/600.)
      RATPSM=FLOAT(NPSM)/(FEEDT/600.)
      RATPA=FLOAT(NPA)/(FEEDT/600.)
      RATPW=FLOAT(NPW)/(FEEDT/600.)
      RATPA=FLOAT(NPA)/(FEEDT/600.)
      RATPR0=FLOAT(NPR0)/(FEEDT/600.)
      RATPR1=FLOAT(NPR1)/(FEEDT/600.)
      RATPR2=FLOAT(NPR2)/(FEEDT/600.)
      RATPR3=FLOAT(NPR3)/(FEEDT/600.)
      RATPR4=FLOAT(NPR4)/(FEEDT/600.)
      RATPR5=FLOAT(NPR5)/(FEEDT/600.)
      RATPR6=FLOAT(NPR6)/(FEEDT/600.)
      RATPR7=FLOAT(NPR7)/(FEEDT/600.)
      RATPR8=FLOAT(NPR8)/(FEEDT/600.)
      RATPR9=FLOAT(NPR9)/(FEEDT/600.)
      NPRT=NPR0+NPR1+NPR2+NPR3+NPR4+NPR5+NPR6+NPR7+NPR8+NPR9
      RATPRT=FLOAT(NPRT)/(FEEDT/600.)
      RATPWE=FLOAT(NPWE)/(FEEDT/600.)


      RATPAB=FLOAT(NPAB)/(FEEDT/600.)
      NPTOT=NP+NPSU+NPSM+NPA+NPW+NPRT+NPWE
      RATPTO=FLOAT(NPTOT)/(FEEDT/600.)
      RATDRI=FLOAT(NDRI)/(FEEDT/600.)
      REALTT=TOTT/10.
      REALFT=FEEDT/10.
      WRITE(6,1000)REALTT,REALFT
 1000 FORMAT(16H TIME ELAPSED = ,F5.1,20H      TIME FEEDING = ,F5.1)
      WRITE(6,1001)
 1001 FORMAT(1HO,9X,4X,1HU,4X,1HD,4X,1HR,2X,3HDRT,2X,3HDRF,2X,3HPET,2X,3
     1HPEF,4X,1HP,2X,3HPSU,2X,3HPSM,3X,2HPA,3X,2HPW)
      WRITE(6,1002)NU,ND,NR,NDROP,NDROP,NPE,NPE,NP,NPSU,NPSM,NPA,NPW
 1002 FORMAT(10H OBS. FREQ,I4,11I5)
      WRITE(6,1003)RATU,RATD,RATR,RATDR1,RATDR2,RATPE1,RATPE2,RATP,RATPS
     1U,RATPSM,RATPA,RATPW
 1003 FORMAT(10H FREQ/MIN ,12F5.1)
      WRITE(6,1012)
 1012 FORMAT(1HO,9X,2X,3HPR0,2X,3HPR1,2X,3HPR2,2X,3HPR3,2X,3HPR4,2X,3HPR
     15,2X,3HPR6,2X,3HPR7,2X,3HPR8,2X,3HPR9,2X,3HPRT,2X,3HPWE,1X,4HPTOT,
     22X,3HPAB,2X,3HDRI)
      WRITE(6,1013)NPR0,NPR1,NPR2,NPR3,NPR4,NPR5,NPR6,NPR7,NPR8,NPR9,NPR
     1T,NPWE,NPTOT,NPAB,NDRI
 1013 FORMAT(10H OBS. FREQ,I4,14I5)
      WRITE(6,1014)RATPR0,RATPR1,RATPR2,RATPR3,RATPR4,RATPR5,RATPR6,RATP
     1R7,RATPR8,RATPR9,RATPRT,RATPWE,RATPTO,RATPAB,RATDRI
 1014 FORMAT(10H FREQ/MIN ,15F5.1)
C
C
C       STATISTICS OUTPUT
C
C
      WRITE(6,1004)
 1004 FORMAT(21H-ACTIVITY SEQUENCE  N,1X,7HSIGMA X,1X,8HSIGMA X2,9X,5HN/
     1MIN,5X,2HAV,10X,2HSS,10X,3HVAR,9X,2HSD,9X,4HVARM,9X,2HSE)
      WRITE(6,1005)
 1005 FORMAT(37HOTIMES FOR UP SORTED BY NEXT ACTIVITY/)
      CALL PSTATS(D,TUD,NUD,RTUD,AVUD)
      CALL PSTATS(R,TUR,NUR,RTUR,AVUR)
      CALL PSTATS(P,TUP,NUP,RTUP,AVUP)
      CALL PSTATS(PSU,TUPSU,NUPSU,RTUPSU,AVUPSU)
      CALL PSTATS(PSM,TUPSM,NUPSM,RTUPSM,AVUPSM)
      CALL PSTATS(PA,TUPA,NUPA,RTUPA,AVUPA)
      CALL PSTATS(PW,TUPW,NUPW,RTUPW,AVUPW)
      CALL PSTATS(PR,TUPR,NUPR,RTUPR,AVUPR)
      CALL PSTATS(PWE,TUPWE,NUPWE,RTUPWE,AVUPWE)
      CALL PSTATS(PAB,TUPAB,NUPAB,RTUPAB,AVUPAB)
      CALL PSTATS(ALL,TU,NU,RTU,AVU)
      WRITE(6,1006)
 1006 FORMAT(39HOTIMES FOR DOWN SORTED BY NEXT ACTIVITY/)
      CALL PSTATS(U,TDU,NDU,RTDU,AVDU)
      CALL PSTATS(R,TDR,NDR,RTDR,AVDR)
      CALL PSTATS(P,TDP,NDP,RTDP,AVDP)
      CALL PSTATS(PSU,TDPSU,NDPSU,RTDPSU,AVDPSU)
      CALL PSTATS(PSM,TDPSM,NDPSM,RTDPSM,AVDPSM)
      CALL PSTATS(PA,TDPA,NDPA,RTDPA,AVDPA)
      CALL PSTATS(PW,TDPW,NDPW,RTDPW,AVDPW)
      CALL PSTATS(PR,TDPR,NDPR,RTDPR,AVDPR)
      CALL PSTATS(PWE,TDPWE,NDPWE,RTDPWE,AVDPWE)
      CALL PSTATS(PAB,TDPAB,NDPAB,RTDPAB,AVDPAB)
      CALL PSTATS(ALL,TD,ND,RTD,AVD)
```

```
      WRITE(6,1007)
 1007 FORMAT(39HOTIMES FOR RUN SORTED BY NEXT ACTIVITY/)
      CALL PSTATS(U,TPU,NRU,RTRU,AVRU)
      CALL PSTATS(D,TRD,NRD,RTRD,AVRD)
      CALL PSTATS(P,TRP,NRP,RTRP,AVRP)
      CALL PSTATS(PSU,TRPSU,NRPSU,RTRPSU,AVRPSU)
      CALL PSTATS(PSM,TRPSM,NRPSM,RTRPSM,AVRPSM)
      CALL PSTATS(PA,TRPA,NRPA,RTRPA,AVRPA)
      CALL PSTATS(PW,TRPW,NRPW,RTRPW,AVRPW)
      CALL PSTATS(PR,TRPR,NRPR,RTRPR,AVRPR)
      CALL PSTATS(PWE,TRPWE,NRPWE,RTRPWE,AVRPWE)
      CALL PSTATS(PAB,TRPAB,NRPAB,RTRPAB,AVRPAB)
      CALL PSTATS(ALL,TR,NR,RTR,AVR)
      WRITE(6,1008)
 1008 FORMAT(27HOPECKING AND HANDLING TIMES/)
      CALL PSTATS(P,TP,NP,RTP,AVP)
      CALL PSTATS(PSU,TPSU,NPSU,RTPSU,AVPSU)
      CALL PSTATS(PSM,TPSM,NPSM,RTPSM,AVPSM)
      CALL PSTATS(PA,TPA,NPA,RTPA,AVPA)
      CALL PSTATS(PW,TPW,NPW,RTPW,AVPW)
      CALL PSTATS(PR0,TPR0,NPR0,RTPR0,AVPR0)
      CALL PSTATS(PR1,TPR1,NPR1,RTPR1,AVPR1)
      CALL PSTATS(PR2,TPR2,NPR2,RTPR2,AVPR2)
      CALL PSTATS(PR3,TPR3,NPR3,RTPR3,AVPR3)
      CALL PSTATS(PR4,TPR4,NPR4,RTPR4,AVPR4)
      CALL PSTATS(PR5,TPR5,NPR5,RTPR5,AVPR5)
      CALL PSTATS(PR6,TPR6,NPR6,RTPR6,AVPR6)
      CALL PSTATS(PR7,TPR7,NPR7,RTPR7,AVPR7)
      CALL PSTATS(PR8,TPR8,NPR8,RTPR8,AVPR8)
      CALL PSTATS(PR9,TPR9,NPR9,RTPR9,AVPR9)
      CALL PSTATS(PWE,TPWE,NPWE,RTPWE,AVPWE)
      CALL PSTATS(PAB,TPAB,NPAB,RTPAB,AVPAB)
      WRITE(6,1009)
 1009 FORMAT(48HOTIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK/)
      CALL PSTATS(P,TPU,NPU,RTPU,AVPU)
      CALL PSTATS(PSU,TPSUU,NPSUU,RTPSUU,AVPSUU)
      CALL PSTATS(PSM,TPSMU,NPSMU,RTPSMU,AVPSMU)
      CALL PSTATS(PA,TPAU,NPAU,RTPAU,AVPAU)
      CALL PSTATS(PW,TPWU,NPWU,RTPWU,AVPWU)
      CALL PSTATS(PRA,TPRAU,NPRAU,RTPRAU,AVPRAU)
      CALL PSTATS(PRB,TPRBU,NPRBU,RTPRBU,AVPRBU)
      CALL PSTATS(PRC,TPRCU,NPRCU,RTPRCU,AVPRCU)
      CALL PSTATS(PWE,TPWEU,NPWEU,RTPWEU,AVPWEU)
      CALL PSTATS(PAB,TPABU,NPABU,RTPABU,AVPABU)
      WRITE(6,1010)
 1010 FORMAT(50HOTIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK/)
      CALL PSTATS(P,TPD,NPD,RTPD,AVPD)
      CALL PSTATS(PSU,TPSUD,NPSUD,RTPSUD,AVPSUD)
      CALL PSTATS(PSM,TPSMD,NPSMD,RTPSMD,AVPSMD)
      CALL PSTATS(PA,TPAD,NPAD,RTPAD,AVPAD)
      CALL PSTATS(PW,TPWD,NPWD,RTPWD,AVPWD)
      CALL PSTATS(PRA,TPRAD,NPRAD,RTPRAD,AVPRAD)
      CALL PSTATS(PRB,TPRBD,NPRBD,RTPRBD,AVPRBD)
      CALL PSTATS(PRC,TPRCD,NPRCD,RTPRCD,AVPRCD)
      CALL PSTATS(PWE,TPWED,NPWED,RTPWED,AVPWED)
      CALL PSTATS(PAB,TPABD,NPABD,RTPABD,AVPABD)
      WRITE(6,1011)
 1011 FORMAT(49HOTIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK/)
      CALL PSTATS(P,TPR,NPR,RTPR,AVPR)
      CALL PSTATS(PSU,TPSUR,NPSUR,RTPSUR,AVPSUR)
      CALL PSTATS(PSM,TPSMR,NPSMR,RTPSMR,AVPSMR)
      CALL PSTATS(PA,TPAR,NPAR,RTPAR,AVPAR)
      CALL PSTATS(PW,TPWR,NPWR,RTPWR,AVPWR)
      CALL PSTATS(PRA,TPRAR,NPRAR,RTPRAR,AVPRAR)
      CALL PSTATS(PRB,TPRBR,NPRBR,RTPRBR,AVPRBR)
      CALL PSTATS(PRC,TPRCR,NPRCR,RTPRCR,AVPRCR)
      CALL PSTATS(PWE,TPWER,NPWER,RTPWER,AVPWER)
      CALL PSTATS(PAB,TPABR,NPABR,RTPABR,AVPABR)
C
C
C       OUTPUT FOR FILE STORAGE
C
C
      IF(MEDIUM.NE.5)GOTO 6001
 6000 READ(5,6003)NDROP,NPE,NDRI,NU,ND,NR,NP,NPSU,NPSM,NPA,NPW,NPR0,NPR1
     1,NPR2,NPR3,NPR4,NPR5,NPR6,NPR7,NPR8,NPR9,NPWE,NPAB
 6003 FORMAT(6X,23I3)
      NPRT=NPR0+NPR1+NPR2+NPR3+NPR4+NPR5+NPR6+NPR7+NPR8+NPR9
      NPTOT=NP+NPSU+NPSM+NPA+NPW+NPRT+NPWE
      REALTT=ZTT
      REALFT=ZFT
      RTUD=AVUD=RTUR=AVUR=RTUP=AVUP=RTUPSU=AVUPSU=0
      RTUPSM=AVUPSM=RTUPA=AVUPA=RTUPW=AVUPW=RTUPR=AVUPR=0
      RTUPWE=AVUPWE=RTUPAB=AVUPAB=0
      RTRU=AVRU=RTRD=AVRD=RTRP=AVRP=RTRPSU=AVRPSU=0
      RTRPSM=AVRPSM=RTRPA=AVRPA=RTRPW=AVRPW=RTRPR=AVRPR=0
      RTRPWE=AVRPWE=RTRPAB=AVRPAB=0
      RTPU=AVPU=RTPSUU=AVPSUU=RTPSMU=AVPSMU=RTPAU=AVPAU=0
      RTPWU=AVPWU=RTPRAU=AVPRAU=RTPRBU=AVPRAU=RTPRCU=AVPRCU=0
      RTPWEU=AVPWEU=RTPABU=AVPABU=RTPR=AVPR=RTPSUR=AVPSUR=0
      RTPSMR=AVPSMR=RTPAR=AVPAR=RTPWR=AVPWR=RTPRAR=AVPRAR=0
      RTPRBR=AVPRBR=RTPRCR=AVPRCR=RTPWER=AVPWER=RTPABR=AVPABR=0
C
C
C       CHANGE REAL VALUES TO APPARENT INTEGER FOR FILE OUTPUT
C
 6001 JAIR=IFIX(AIRT)
      JMUDT=IFIX(AMUDT)
      JT1=IFIX(HT1)
      JT2=IFIX(HT2)
C
C
      NSER=1
      WRITE(7,19)NCASE,NSER,NC,MEDIUM,MSP,NSEX,NAGE,NDAYS,NFOOT,NDIST,ND
     1IST2,NFLOCK,NPOS,LOC,NSTAT,NTIM,NDATE,NRAIN,NCLOUD,NWIND,NDIR,JAIR
     2,JMUDT,HW1,JT1,HW2,JT2,INDIV,NEARSP,NWET
   19 FORMAT(I4,I2,I2,4I1,I2,I1,3I3,I1,I2,I1,I4,I6,I1,I1,I2,I1,I3,I3,I4,
     1I3,I4,I3,I4,I2,I1)
      NSER=71
      WRITE(7,2001)NCARD,NSER,REALTT,REALFT,NDROP,NPE,NDRI,NPRT,NPTOT
 2001 FORMAT(I4,I2,2F6.1,3I2,2I3)
      NSER=72
      WRITE(7,2000)NCARD,NSER,NUD,RTUD,AVUD,NUR,RTUR,AVUR,NUP,RTUP,AVUP,
     1NUPSU,RTUPSU,AVUPSU
      NSER=73
      WRITE(7,2000)NCARD,NSER,NUPSM,RTUPSM,AVUPSM,NUPA,RTUPA,AVUPA,NUPW,
     1RTUPW,AVUPW,NUPR,RTUPR,AVUPR
      NSER=74
      WRITE(7,2000)NCARD,NSER,NUPWE,RTUPWE,AVUPWE,NUPAB,RTUPAB,AVUPAB,NU
     1,RTU,AVU,ND,RTD,AVD
```

```
1021              NSER=75
1022              WRITE(7,2000)NCARD,NSER,NRU,RTRU,AVRU,NRD,RTRD,AVRD,NRP,RTRP,AVRP,
1023             1NRPSU,RTRPSU,AVRPSU
1024              NSER=76
1025              WRITE(7,2000)NCARD,NSER,NRPSM,RTRPSM,AVRPSM,NRPA,RTRPA,AVRPA,NRPW,
1026             1RTRPW,AVRPW,NRPR,RTRPR,AVRPR
1027              NSER=77
1028              WRITE(7,2000)NCARD,NSER,NRPWE,RTRPWE,AVRPWE,NRPAB,RTRPAB,AVRPAB,NR
1029             1,RTR,AVR,NP,RTP,AVP
1030              NSER=78
1031              WRITE(7,2000)NCARD,NSER,NPSU,RTPSU,AVPSU,NPSM,RTPSM,AVPSM,NPA,RTPA
1032             1,AVPA,NPW,RTPW,AVPW
1033              NSER=79
1034              WRITE(7,2000)NCARD,NSER,NPR0,RTPR0,AVPR0,NPR1,RTPR1,AVPR1,NPR2,RTP
1035             1R2,AVPR2,NPR3,RTPR3,AVPR3
1036              NSER=80
1037              WRITE(7,2000)NCARD,NSER,NPR4,RTPR4,AVPR4,NPR5,RTPR5,AVPR5,NPR6,RTP
1038             1R6,AVPR6,NPR7,RTPR7,AVPR7
1039              NSER=81
1040              WRITE(7,2000)NCARD,NSER,NPR8,RTPR8,AVPR8,NPR9,RTPR9,AVPR9,NPWE,RTP
1041             1WE,AVPWE,NPAB,RTPAB,AVPAB
1042              NSER=82
1043              WRITE(7,2000)NCARD,NSER,NPU,RTPU,AVPU,NPSUU,RTPSUU,AVPSUU,NPSMU,RT
1044             1PSMU,AVPSMU,NPAU,RTPAU,AVPAU
1045              NSER=83
1046              WRITE(7,2000)NCARD,NSER,NPWU,RTPWU,AVPWU,NPRAU,RTPRAU,AVPRAU,NPRBU
1047             1,RTPRBU,AVPRBU,NPRCU,RTPRCU,AVPRCU
1048              NSER=84
1049              WRITE(7,2000)NCARD,NSER,NPWEU,RTPWEU,AVPWEU,NPABU,RTPABU,AVPABU,NP
1050             1R,RTPR,AVPR,NPSUR,RTPSUR,AVPSUR
1051              NSER=85
1052              WRITE(7,2000)NCARD,NSER,NPSMR,RTPSMR,AVPSMR,NPAR,RTPAR,AVPAR,NPWR,
1053             1RTPWR,AVPWR,NPRAR,RTPRAR,AVPRAR
1054              NSER=86
1055              WRITE(7,2000)NCARD,NSER,NPRBR,RTPRBR,AVPRBR,NPRCR,RTPRCR,AVPRCR,NP-
1056             1WER,RTPWER,AVPWER,NPABR,RTPABR,AVPABR
1057         2000 FORMAT(I4,I2,4(I3,F6.2,F9.3))
1058              GOTO 1
1059              END
1060       C
1061       C
1062       C
1063              SUBROUTINE PSTATS(ITEM,A,N,SSUMA,SSUMA2)
1064              COMMON FEEDT
1065              DIMENSION A(20)
1066              REAL*8 SUMA,SUMA2,SSA
1067              T=FEEDT/600.
1068       C
1069       C       SET ZEROS
1070       C
1071              SUMA=0
1072              SUMA2=0
1073              SSUMA=0
1074              SSUMA2=0
1075       C
1076       C       LOOP FOR SUM AND SUM OF SQUARES
1077       C
1078              IF(N.LT.1)GOTO 15
1079              DO 10 I=1,N
1080              SUMA=SUMA+A(I)/10
1081              SUMA2=SUMA2+A(I)*A(I)/100
1082           10 CONTINUE
1083       C
1084       C       CALCULATE
1085       C
1086              SSUMA=SUMA
1087              SSUMA2=SUMA2
1088              AVA=SUMA/FLOAT(N)
1089              SSA=SUMA2-SUMA*SUMA/FLOAT(N)
1090              IF(N.EQ.1)GOTO 21
1091              VARA=SSA/(FLOAT(N)-1)
1092              IF(VARA.LE.0)VARA=0
1093              GOTO 20
1094           21 VARA=0.
1095              GOTO 20
1096           20 SDA=SQRT(VARA)
1097              VARMA=VARA/FLOAT(N)
1098              IF(VARMA.LE.0)VARMA=0
1099              SEA=SQRT(VARMA)
1100              RATN=FLOAT(N)/T
1101       C
1102       C       PRINT RESULT
1103       C
1104              WRITE(6,100)ITEM,N,SSUMA,SSUMA2,RATN,AVA,SSA,VARA,SDA,VARMA,SEA
1105          100 FORMAT(1H ,A4,10X,I3,F6.1,8F12.3)
1106              RETURN
1107           15 WRITE(6,101)ITEM
1108          101 FORMAT(1H ,A4,8X,4HZERO)
1109              RETURN
1110              END
1111       $DATA
1112       $STOP
END OF FILE
```

SECTION 4. EXAMPLE OF INPUT OF OBSERVATIONS ON DURATIONS OF EACH ACTIVITY

```
0436010911101 21 -1 -1   3004117050306750 58 86    0900111214511169 34 12
043602   U      8D       3P       4U       9R       7U      20R      4D      16P      10
043603   R      4U      13R       7U      18R       6P       3R      4U       7R      12
043604   U     35R      10U      10R       7P       3U       9R      3P       4U      23
043605   R      8U      23R      13U      25R      14D       2P      4R       2U      16
043606   R      4D       7P      10P       3R      10U       9R      6D      14P      12
043607   P      8P      17P       7P       9P       9R       3U     24R      4D       5
043608   P     15P       8P      13R       8U      15R      12U      8P      5U      23
043609   R     10U      17R      10U      10R       9P       3R      7U     22R      19
043610   U     16R      22U      23R      20U     21STOP
0437010711101 21 -1 -1   3004118300306750 2 38 86    0900111214511169 34 12
043702   PSM   18PSM     8R       3U      13R       4U       9R     3PSM     2U      18
043703   R      8U      17R       3U      18R       8U      19R      11U     11R       6
043704   D      2PSM     3U      21R      13U      11R       6U       6R     2PSM      3
043705   U     22R       5U      21R       9U      17R      2PSM      3R      6U      18
043706   R     10U      11R       8U      13R       4PSM     5R      10U     14R       6
043707   PSM    3R       4U      21R       4U      10R       3D      11PSM   25PSM    10
043708   PSM   14R       5PSM     4U      20STOP
0438010511101 21 -1 -1   3004118340306750 2 38 86    0900111214511169 35 12
043802   U     20R      17U      18R       8U      19R       3U     17R       2D       7
043803   P      6U      11P       3U      13R       3PSM     3U      10PSM    3U       4
043804   PSM    3U      23R       3P       6R       2U      17R     17U      16R       5
043805   U     10R       4P       6U      13P       6R       6U     28R      4U      24
043806   R      8U      15R       7U      12R      11U      33R      3P      47STOP
0439010611101 21 -1 -1   3004119060306750 2 38 86    0900111214511169 35 12
043902   R     10U       7R       8D       2P       3R      17U      7R       5U      12
043903   R      2P       3U      12R      17U      12R       4U     12D       6P       4
043904   U     25D       2P       3R       4U      10R       7U      9DR      7R       3
043905   D      4P       7R       7U      11R       3U      14R      3P       3R       8
043906   U     18R       5D       8U       5R       4U      23R      4U      12R      10
043907   U      5R       2P       2R      10U     13STOP
0440011111114-10 -1 -1   1004119370306750 0 38 62    0900111214511175 15 10
044002   U     20R       5U      12R       2P       4R       4U     23R      10U      21
044003   R     10U      19R       6U       8PR4    20R       3U     12R       3P       5
044004   R      2U       8PR2    35R       2U      22R       7P      4U       9P       3
044005   U     10PR0     6R       2U      21R       2U      11R      3P       3R       2
044006   U     16R       6P       3R       3U      16R       5U     15R       2P       2
044007   R      2U      14R       3P       7R       2U      10R      2P       7U      16
044008   R      4PR0     4R       3U      31R       2P       3R      4U      30R       2
044009   PSU   29R       2U      18PSU     2R       2U       7PSU    3R       4U      27
044010   R      6U      28R       3P       3R       4U      15R      4P       4R       6
044011   U     11R       3P       2R       2U      18R       7U     33R      3P       3
044012   R      3U      16R       2P       3R       9U      15STOP
-109
```

```
207401022103281100 10  303410935150875                 083911621101146975 8100100010
207402   R       8U     0R       5PSM    0U      0R       3PSM    0U       0R       5
207403   U       0R     6U       0STOP
207501032103281   3  3  303410950150875                 083911621101146969 1200400040
207502   R       5U     0R       5PSU    0U      0R       5U      0R       1P       0
207503   R       2U     0R       3U      0R     20U       0R     50U       0R       5
207504   U       0STOP
207601062103281   3  3  303411008150875                 08391162110114     1100530053
207602   R       3P     0U       0R      6U      0P       0U      0R       3U       0
207603   R       4U     0R       2P      0R      3U       0R      3P       0R       2
207604   U       0R     6U       0R      3P      0R       2U      0R       3P       0
207605   R       3U     0R       3U      0R      2P       0R      3U       0R       3
207606   P       0U     0R       1P      0R      2U       0R      2PSU     0R       3
207607   U       0R     5U       0R      3U      0R       4U      0STOP
207701062114-11   3  3  403411010150875                 083911621101147549 1000430043
207702   R       8U     0PSU     0R      3U      0R       3U      0R       2PSU     0
207703   R       3U     0R       3PSU    0U      0R       3U      0R       3PSU     0
207704   R       6U     0R       6U      0R      2U       0R      6U       0R       5
207705   PSU     0R     2U       0R      2U      0R       5PSU    0R       8U       0
207706   R      10U     0R       3PSU    0U      0R       7U      0PSU     0R       2
207707   U       0STOP
207801052101170 -1 -1  203211211150875                 083911621101147552 1000360036
207802   R       3P     0R       8U      0R      3U       0R      1U       0R       5
207803   U       0P     0R       4U      0R      5P       0R      2U       0R       2
207804   P       0R     1U       0R      1P      0U       0R      1P       0U       0
207805   R       3D     0P       0U      0R      3P       0R      1P       0U       0
207806   P       0R     3U       0R      1P      0R       3U      0STOP
207901022101170 -1 -1  203211223150875                 083911621101147552 1000180018
207902   R       5P     0R       2U      0R      3U       0R      1P       0R       2
207903   U       0R     1P       0U      0R     15U       0SI     0STOP
208001052124-11   8  8  100411004170875026 8134         222611411121157516 1100470047
208002   P       0R     5U       0R      7U      0PW      0U      0R       8U       0
208003   P       0R     2U       0P      0R      6U       0R      3P       0R       4
208004   U       0R     6P       0R      4U      0R       8U      0P       0R       2
208005   U       0R     3P       0U      0R      2P       0R      4U       0R       6
208006   U       0R     9U       0R      5U      0STOP
-109
```

SECTION 6. EXAMPLE OF INPUT OF OBSERVATIONS OF FREQUENCIES OF PECKING, ETC. ONLY

```
519101015104-10 -1 -1  701701007250974O6 23      10011102223111     1000600060
519102                          9
519201015104-10 -1 -1  701701008250974O6 23      10011102223111     1000600060
519202                         70
519301015103-10 -1 -1  701701012250974O6 23      10011102223111     1000900090
519302                         24
519401015104-10 -1 -1  701701012250974O6 23      10011102223111     1000600060
519402                         61                1
519501015103-10 -1 -1  701701013250974O6 23      10011102223111     1000600060
519502                         71
519601015103-10 -1 -1  701701014250974O6 23      10011102223111     1000240024
519602                         23
519701015104-10 -1 -1 1001701100250974O6 23      10011102223111     1000600060
519702                         94
519801015104-10 -1 -1 1001701101250974O6 23      10011102223111     1000600060
519802                         13
519901015104-10 -1 -1 1001701115250974O6 23      10011102223111     1000200020
519902                          3
520001015202-10 -1 -1  101701125250974O8 23      10011102223111     1000600060
520002                          4
-109
```

```
CASE NO.  436 . 10 INITIAL DATA CARDS.    T/TI

RINGED PLOVER
INDIVIDUAL NO.6934
SEX     .  AGE CODE 1 (CHICK AGE  2 DAYS). STATUS: 1, LOCATION CODE:  4, TIME: 1705, DATE:  30675

RAIN CODE: 0, CLOUD: 5/8, WIND FORCE:  5 FROM NW  , AIR TEMP:  8.6, SUBSTRATE TEMP:  0.0, HW AT  900 ( 11.1 ) AND 2145 ( 11.1 )
FOOTSHAKE: 1, DISTANCE FROM NEAREST SAME SP:  -1 M, OTHER SP:  -1 M, FLOCK SIZE:   3, POSITION IN FLOCK: 0

INDIVIDUAL CODE NO. 6934
TIME ELAPSED =  84.3      TIME FEEDING =  34.3

                U     D     R   DRT   DRF   PET   PEF     P   PSU   PSM    PA    PW
OBS. FREQ      24     6    28     0     0     0     0    19     0     0     0     0
FREQ/MIN     17.1   4.3  19.9   0.0   0.0   0.0   0.0  13.5   0.0   0.0   0.0   0.0

               PR0   PR1   PR2   PR3   PR4   PR5   PR6   PR7   PR8   PR9   PRT   PWE  PTOT   PAB   DRI
OBS. FREQ        0     0     0     0     0     0     0     0     0     0     0     0    19     0     0
FREQ/MIN       0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0  13.5   0.0   0.0

ACTIVITY SEQUENCE  N SIGMA X SIGMA X2          N/MIN      AV          SS         VAR        SD        VARM       SE

TIMES FOR UP SORTED BY NEXT ACTIVITY

D                  1   0.8      0.640          0.712     0.800       0.000      0.000     0.000     0.000     0.000
R                 21  36.7     74.370         14.947     1.748      10.232      0.512     0.715     0.024     0.155
P                  1   0.8      0.640          0.712     0.800       0.000      0.000     0.000     0.000     0.000
PSU          ZERO
PSM          ZERO
PA           ZERO
PW           ZERO
PR           ZERO
PWE          ZERO
PAB          ZERO
ALL               24  40.4     80.060         17.082     1.683      12.053      0.524     0.724     0.022     0.148

TIMES FOR DOWN SORTED BY NEXT ACTIVITY

U            ZERO
R            ZERO
P                  6   4.7      5.390          4.270     0.783       1.708      0.342     0.585     0.057     0.239
PSU          ZERO
PSM          ZERO
PA           ZERO
PW           ZERO
PR           ZERO
PWE          ZERO
PAB          ZERO
ALL                6   4.7      5.390          4.270     0.783       1.708      0.342     0.585     0.057     0.239

TIMES FOR RUN SORTED BY NEXT ACTIVITY

U                 19  18.8     24.220         13.523     0.989       5.618      0.312     0.559     0.016     0.128
D                  5   3.2      2.800          3.559     0.640       0.752      0.188     0.434     0.038     0.194
P                  4   2.5      1.750          2.847     0.625       0.187      0.062     0.250     0.016     0.125
PSU          ZERO
PSM          ZERO
PA           ZERO
PW           ZERO
```

PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	28	24.5	28.770	19.929	0.875	7.333	0.272	0.521	0.010	0.098

PECKING AND HANDLING TIMES

P	19	14.7	14.750	13.523	0.774	3.377	0.188	0.433	0.010	0.099
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PR0	ZERO									
PR1	ZERO									
PR2	ZERO									
PR3	ZERO									
PR4	ZERO									
PR5	ZERO									
PR6	ZERO									
PR7	ZERO									
PR8	ZERO									
PR9	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK

P	4	6.4	12.200	2.847	1.600	1.960	0.653	0.808	0.163	0.404
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO									
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK

P	7	3.8	2.580	4.982	0.543	0.517	0.086	0.294	0.012	0.111
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

CASE NO. 437 , 10 INITIAL DATA CARDS, T/TI

RINGED PLOVER
INDIVIDUAL NO.6934
SEX , AGE CODE 1 (CHICK AGE 2 DAYS), STATUS: 1, LOCATION CODE: 4, TIME: 1830, DATE: 30675

RAIN CODE: 0, CLOUD: 2/8, WIND FORCE: 3 FROM NW , AIR TEMP: 8.6, SUBSTRATE TEMP: 0.0, HW AT 900 (11.1) AND 2145 (11.1)
FOOTSHAKE: 1, DISTANCE FROM NEAREST SAME SP: -1 M, OTHER SP: -1 M, FLOCK SIZE: 3, POSITION IN FLOCK: 0

INDIVIDUAL CODE NO. 6934
TIME ELAPSED = 56.4 TIME FEEDING = 56.4

	U	D	R	DRT	DRF	PET	PEF	P	PSU	PSM	PA	PW
OBS. FREQ	20	2	24	0	0	0	0	0	0	12	0	0
FREQ/MIN	21.3	2.1	25.5	0.0	0.0	0.0	0.0	0.0	0.0	12.8	0.0	0.0

	PR0	PR1	PR2	PR3	PR4	PR5	PR6	PR7	PR8	PR9	PRT	PWE	PTOT	PAB	DRI
OBS. FREQ	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0
FREQ/MIN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.8	0.0	0.0

ACTIVITY SEQUENCE	N	SIGMA X	SIGMA X2	N/MIN	AV	SS	VAR	SD	VARM	SE
TIMES FOR UP SORTED BY NEXT ACTIVITY										
D	ZERO									
R	19	29.0	48.320	20.213	1.526	4.057	0.225	0.475	0.012	0.109
P	ZERO									
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	20	31.0	52.320	21.277	1.550	4.270	0.225	0.474	0.011	0.106
TIMES FOR DOWN SORTED BY NEXT ACTIVITY										
U	ZERO									
R	ZERO									
P	ZERO									
PSU	ZERO									
PSM	2	1.3	1.250	2.128	0.650	0.405	0.405	0.636	0.202	0.450
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	2	1.3	1.250	2.128	0.650	0.405	0.405	0.636	0.202	0.450
TIMES FOR RUN SORTED BY NEXT ACTIVITY										
U	16	11.2	9.260	17.021	0.700	1.420	0.095	0.308	0.006	0.077
D	2	0.9	0.450	2.128	0.450	0.045	0.045	0.212	0.023	0.150
P	ZERO									
PSU	ZERO									
PSM	6	2.2	0.940	6.383	0.367	0.133	0.027	0.163	0.004	0.067
PA	ZERO									
PW	ZERO									

PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	24	14.3	10.650	25.532	0.596	2.130	0.093	0.304	0.004	0.062

PECKING AND HANDLING TIMES

P	ZERO									
PSU	ZERO									
PSM	12	9.8	13.900	12.766	0.817	5.897	0.536	0.732	0.045	0.211
PA	ZERO									
PW	ZERO									
PR0	ZERO									
PR1	ZERO									
PR2	ZERO									
PR3	ZERO									
PR4	ZERO									
PR5	ZERO									
PR6	ZERO									
PR7	ZERO									
PR8	ZERO									
PR9	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO									
PSU	ZERO									
PSM	4	8.1	16.490	4.255	2.025	0.088	0.029	0.171	0.007	0.085
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO									
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO									
PSU	ZERO									
PSM	5	2.8	1.860	5.319	0.560	0.292	0.073	0.270	0.015	0.121
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

SECTION 8. EXAMPLE OF PRINTED OUTPUT FROM PLOVP2 FOR SECTION-4-TYPE INPUT

```
CASE NO.  436 , 10 INITIAL DATA CARDS,   T/TI .          RUNS INCLUDED IN PECK-TIME

RINGED PLOVER
INDIVIDUAL NO.6934
SEX     ,  AGE CODE 1 (CHICK AGE  2 DAYS), STATUS: 1, LOCATION CODE:  4, TIME: 1705, DATE:  30675

RAIN CODE: 0, CLOUD: 5/8, WIND FORCE:  5 FROM NW  , AIR TEMP:  8.6, SUBSTRATE TEMP:  0.0, HW AT  900 ( 11.1 ) AND 2145 ( 11.1 )
FOOTSHAKE: 1, DISTANCE FROM NEAREST SAME SP:  -1 M, OTHER SP:  -1 M, FLOCK SIZE:   3, POSITION IN FLOCK: 0

INDIVIDUAL CODE NO. 6934

RECODED DATA:
U      8.    D      3.    P      4.    U      9.    R      7.    U     20.    R      4.    D     16.    P     14.
U     13.    R      7.    U     18.    P     13.    U      7.    R     12.    U     35.    R     10.    U     10.
P     10.    U      9.    P      7.    U     23.    R      8.    U     23.    P     13.    U     25.    R     14.
D      2.    P      6.    U     16.    R      4.    D      7.    P     10.    P     13.    U      9.    R      6.
D     14.    P     12.    P      8.    P     17.    P      7.    P      9.    P     12.    U     24.    R      4.
D      5.    P     15.    P      8.    P     21.    U     15.    R     12.    U      8.    P      5.    U     23.
R     10.    U     17.    R     10.    U     10.    P     19.    U     22.    R     19.    U     16.    R     22.
U     23.    R     20.    U     21.    STOP   0.
TIME ELAPSED =   84.3      TIME FEEDING =   84.3

              U     D     R   DRT   DRF   PET   PEF     P   PSU   PSM    PA    PW
OBS. FREQ    24     6    17     0     0     0     0    19     0     0     0     0
FREQ/MIN   17.1   4.3  12.1   0.0   0.0   0.0   0.0  13.5   0.0   0.0   0.0   0.0

              PR0   PR1   PR2   PR3   PR4   PR5   PR6   PR7   PR8   PR9   PRT   PWE  PTOT   PAB   DRI
OBS. FREQ       0     0     0     0     0     0     0     0     0     0     0     0    19     0     0
FREQ/MIN      0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0   0.0  13.5   0.0   0.0

ACTIVITY SEQUENCE  N SIGMA X SIGMA X2          N/MIN      AV          SS          VAR         SD          VARM        SE
TIMES FOR UP SORTED BY NEXT ACTIVITY
D                  1   0.8      0.640          0.712     0.800       0.000       0.000       0.000       0.000       0.000
R                 17  32.0     68.320         12.100     1.882       8.085       0.505       0.711       0.030       0.172
P                  5   5.5      6.690          3.559     1.100       0.640       0.160       0.400       0.032       0.179
PSU           ZERO
PSM           ZERO
PA            ZERO
PW            ZERO
PR            ZERO
PWE           ZERO
PAB           ZERO
ALL               24  40.4     80.060         17.082     1.683      12.053       0.624       0.724       0.022       0.148
TIMES FOR DOWN SORTED BY NEXT ACTIVITY
U             ZERO
R             ZERO
P                  6   4.7      5.390          4.270     0.783       1.708       0.342       0.585       0.057       0.239
PSU           ZERO
PSM           ZERO
PA            ZERO
PW            ZERO
PR            ZERO
PWE           ZERO
PAB           ZERO
ALL                6   4.7      5.390          4.270     0.783       1.708       0.342       0.585       0.057       0.239
```

TIMES FOR RUN SORTED BY NEXT ACTIVITY

U	12	15.0	21.640	8.541	1.250	2.890	0.263	0.513	0.022	0.148
D	5	3.2	2.800	3.559	0.640	0.752	0.188	0.434	0.038	0.194
P	ZERO									
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	17	18.2	24.440	12.100	1.071	4.955	0.310	0.557	0.018	0.135

PECKING AND HANDLING TIMES

P	19	21.0	27.220	13.523	1.105	4.009	0.223	0.472	0.012	0.108
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PR0	ZERO									
PR1	ZERO									
PR2	ZERO									
PR3	ZERO									
PR4	ZERO									
PR5	ZERO									
PR6	ZERO									
PR7	ZERO									
PR8	ZERO									
PR9	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK

P	11	17.0	30.600	7.829	1.545	4.327	0.433	0.658	0.039	0.198
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO
PSU	ZERO
PSM	ZERO
PA	ZERO
PW	ZERO
PRA	ZERO
PRB	ZERO
PRC	ZERO
PWE	ZERO
PAB	ZERO

TIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO
PSU	ZERO
PSM	ZERO
PA	ZERO
PW	ZERO
PRA	ZERO
PRB	ZERO
PRC	ZERO
PWE	ZERO
PAB	ZERO

CASE NO. 437 , 8 INITIAL DATA CARDS, T/TI RUNS INCLUDED IN PECK-TIME

RINGED PLOVER
INDIVIDUAL NO.6934
SEX , AGE CODE 1 (CHICK AGE 2 DAYS), STATUS: 1, LOCATION CODE: 4, TIME: 1830, DATE: 30675

RAIN CODE: 0, CLOUD: 2/8, WIND FORCE: 3 FROM NW , AIR TEMP: 8.6, SUBSTRATE TEMP: 0.0, HW AT 900 (11.1) AND 2145 (11.1)
FOOTSHAKE: 1, DISTANCE FROM NEAREST SAME SP: -1 M, OTHER SP: -1 M, FLOCK SIZE: 3, POSITION IN FLOCK: 0

INDIVIDUAL CODE NO. 6934

RECODED DATA:

PSM	18.	PSM	11.	U	13.	R	4.	U	9.	PSM	5.	U	18.	R	8.	U	17.
R	3.	U	18.	R	8.	U	19.	R	11.	U	11.	R	6.	D	2.	PSM	3.
U	21.	R	13.	U	11.	R	6.	U	6.	PSM	5.	U	22.	R	5.	U	21.
R	9.	U	17.	PSM	11.	U	18.	R	10.	U	11.	R	8.	U	13.	PSM	19.
U	14.	PSM	13.	U	21.	R	4.	U	10.	R	3.	D	11.	PSM	25.	PSM	10.
PSM	14.	PSM	9.	U	20.	STOP	0.										

TIME ELAPSED = 56.4 TIME FEEDING = 56.4

	U	D	R	DRT	DRF	PET	PEF	P	PSU	PSM	PA	PW
OBS. FREQ	20	2	14	0	0	0	0	0	0	12	0	0
FREQ/MIN	21.3	2.1	14.9	0.0	0.0	0.0	0.0	0.0	0.0	12.8	0.0	0.0

	PR0	PR1	PR2	PR3	PR4	PR5	PR6	PR7	PR8	PR9	PRT	PWE	PTOT	PAB	DRI
OBS. FREQ	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0
FREQ/MIN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.8	0.0	0.0

ACTIVITY SEQUENCE	N	SIGMA X	SIGMA X2	N/MIN	AV	SS	VAR	SD	VARM	SE
TIMES FOR UP SORTED BY NEXT ACTIVITY										
D	ZERO									
R	14	23.1	40.610	14.894	1.650	2.495	0.192	0.438	0.014	0.117
P	ZERO									
PSU	ZERO									
PSM	5	5.9	7.710	5.319	1.180	0.748	0.187	0.432	0.037	0.193
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	20	31.0	52.320	21.277	1.550	4.270	0.225	0.474	0.011	0.105
TIMES FOR DOWN SORTED BY NEXT ACTIVITY										
U	ZERO									
R	ZERO									
P	ZERO									
PSU	ZERO									
PSM	2	1.3	1.250	2.128	0.650	0.405	0.405	0.636	0.202	0.450
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	2	1.3	1.250	2.128	0.650	0.405	0.405	0.636	0.202	0.450

TIMES FOR RUN SORTED BY NEXT ACTIVITY

U	12	8.9	7.650	12.766	0.742	1.049	0.095	0.309	0.008	0.089
D	2	0.9	0.450	2.128	0.450	0.045	0.045	0.212	0.023	0.159
P	ZERO									
PSU	ZERO									
PSM	ZERO									
PA	ZERO									
PW	ZERO									
PR	ZERO									
PWE	ZERO									
PAB	ZERO									
ALL	14	9.8	8.100	14.894	0.700	1.240	0.095	0.309	0.007	0.093

PECKING AND HANDLING TIMES

P	ZERO									
PSU	ZERO									
PSM	12	14.3	21.570	12.766	1.192	4.529	0.412	0.642	0.034	0.185
PA	ZERO									
PW	ZERO									
PR0	ZERO									
PR1	ZERO									
PR2	ZERO									
PR3	ZERO									
PR4	ZERO									
PR5	ZERO									
PR6	ZERO									
PR7	ZERO									
PR8	ZERO									
PR9	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF UP SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO									
PSU	ZERO									
PSM	8	14.7	27.790	8.511	1.837	0.779	0.111	0.334	0.014	0.118
PA	ZERO									
PW	ZERO									
PRA	ZERO									
PRB	ZERO									
PRC	ZERO									
PWE	ZERO									
PAB	ZERO									

TIMES OF DOWN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO
PSU	ZERO
PSM	ZERO
PA	ZERO
PW	ZERO
PRA	ZERO
PRB	ZERO
PRC	ZERO
PWE	ZERO
PAB	ZERO

TIMES OF RUN SORTED BY OUTCOME OF PRECEDING PECK

P	ZERO
PSU	ZERO
PSM	ZERO
PA	ZERO
PW	ZERO
PRA	ZERO
PRB	ZERO
PRC	ZERO
PWE	ZERO
PAB	ZERO

SECTION 9. EXAMPLE OF OUTPUT TO COMPUTER FILE FROM PLOVPROG

```
436 1 91101 21 -1 -1  30 411705 3067505 58 86  0 900111214511169934 12
43671  84.3  84.3 0 0 0  0 19
43672   1  0.80    0.640 21 36.70   74.370  1  0.80    0.640  0  0.00    0.000
43673   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43674   0  0.00    0.000  0  0.00    0.000 24 40.40   30.060  6  4.70    5.330
43675  19 18.80   24.220  5  3.20    2.800  4  2.50    1.750  0  0.00    0.000
43676   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43677   0  0.00    0.000  0  0.00    0.000 28 24.50   28.770 19 14.70   14.750
43678   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43679   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43680   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43681   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43682   4  6.40   12.200  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43683   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43684   0  0.00    0.000  0  0.00    0.000  7  3.80    2.530  0  0.00    0.000
43685   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43686   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
437 1 91101 21 -1 -1  30 411830 3067502 38 86  0 900111214511169934 12
43771  56.4  56.4 0 0 0  0 12
43772   0  0.00    0.000 14 29.00   48.320  0  0.00    0.000  0  0.00    0.000
43773   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43774   0  0.00    0.000  0  0.00    0.000 20 31.00   52.320  2  1.30    1.250
43775  16 11.20    9.260  2  0.90    0.450  0  0.00    0.000  0  0.00    0.000
43776   6  2.20    0.940  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43777   0  0.00    0.000  0  0.00    0.000 24 14.30   10.650  0  0.00    0.000
43778   0  0.00    0.000 12  9.80   13.900  0  0.00    0.000  0  0.00    0.000
43779   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43780   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43781   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43782   0  0.00    0.000  0  0.00    0.000  4  8.10   16.490  0  0.00    0.000
43783   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43784   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43785   5  2.80    1.360  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
43786   0  0.00    0.000  0  0.00    0.000  0  0.00    0.000  0  0.00    0.000
```

Appendix 4. Scattergrams relating feeding rates and foraging behaviour of Ringed Plover chicks to age and environmental conditions (see Paper 3).

On these plots, single points are represented by asterisks, from 2 to 8 coincident points by the numbers of such points, and 9 or more coincident points by '9'. On some figures the mean (± 1 s.e.) value for adults (A) in the same area is also indicated.

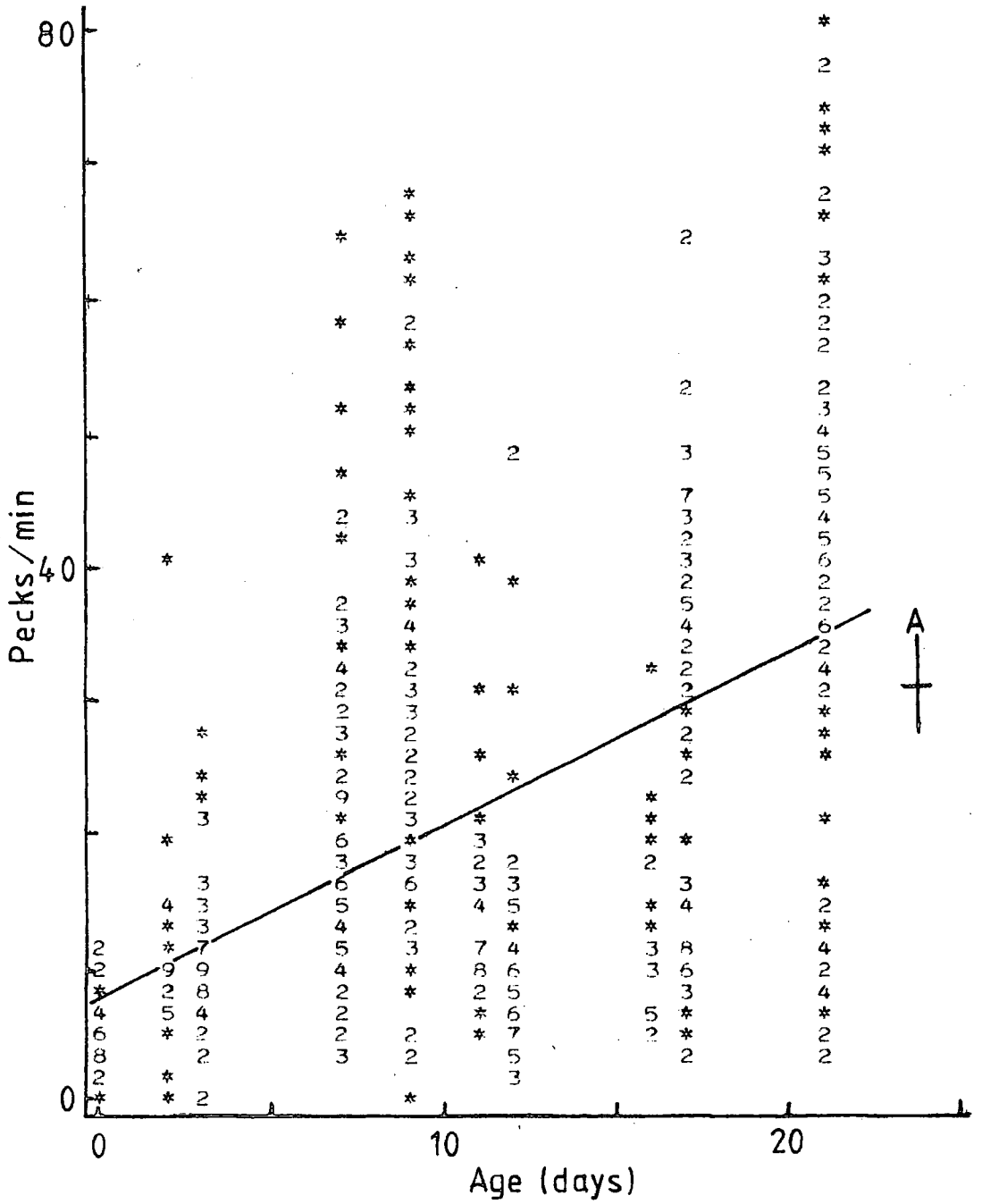


Figure 1. Rate of pecking by chicks at Mestersvig in relation to age.

Fitted regression line is $y = 1.30x + 8.00$ ($r = 0.49$; $P < 0.00001$).

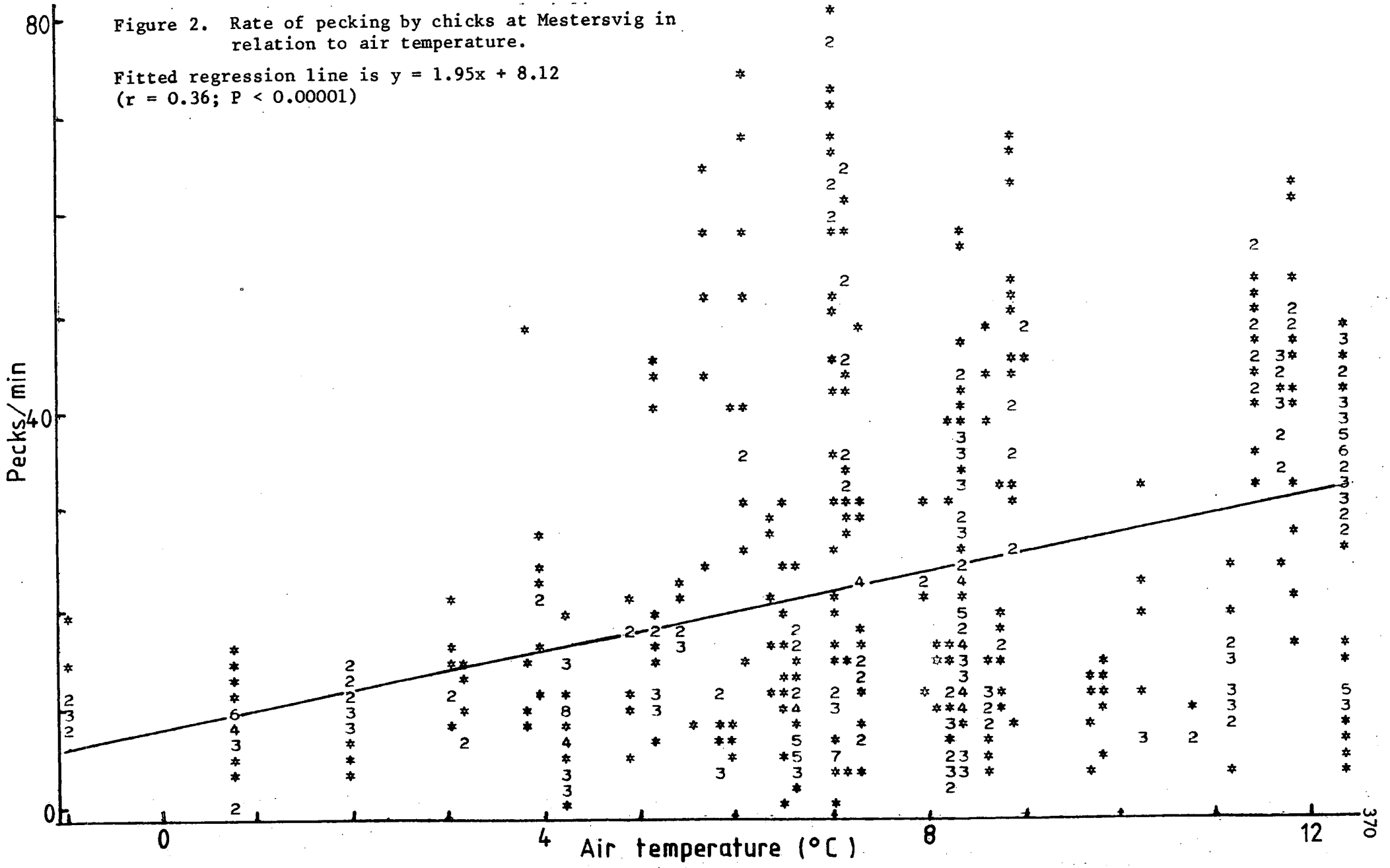
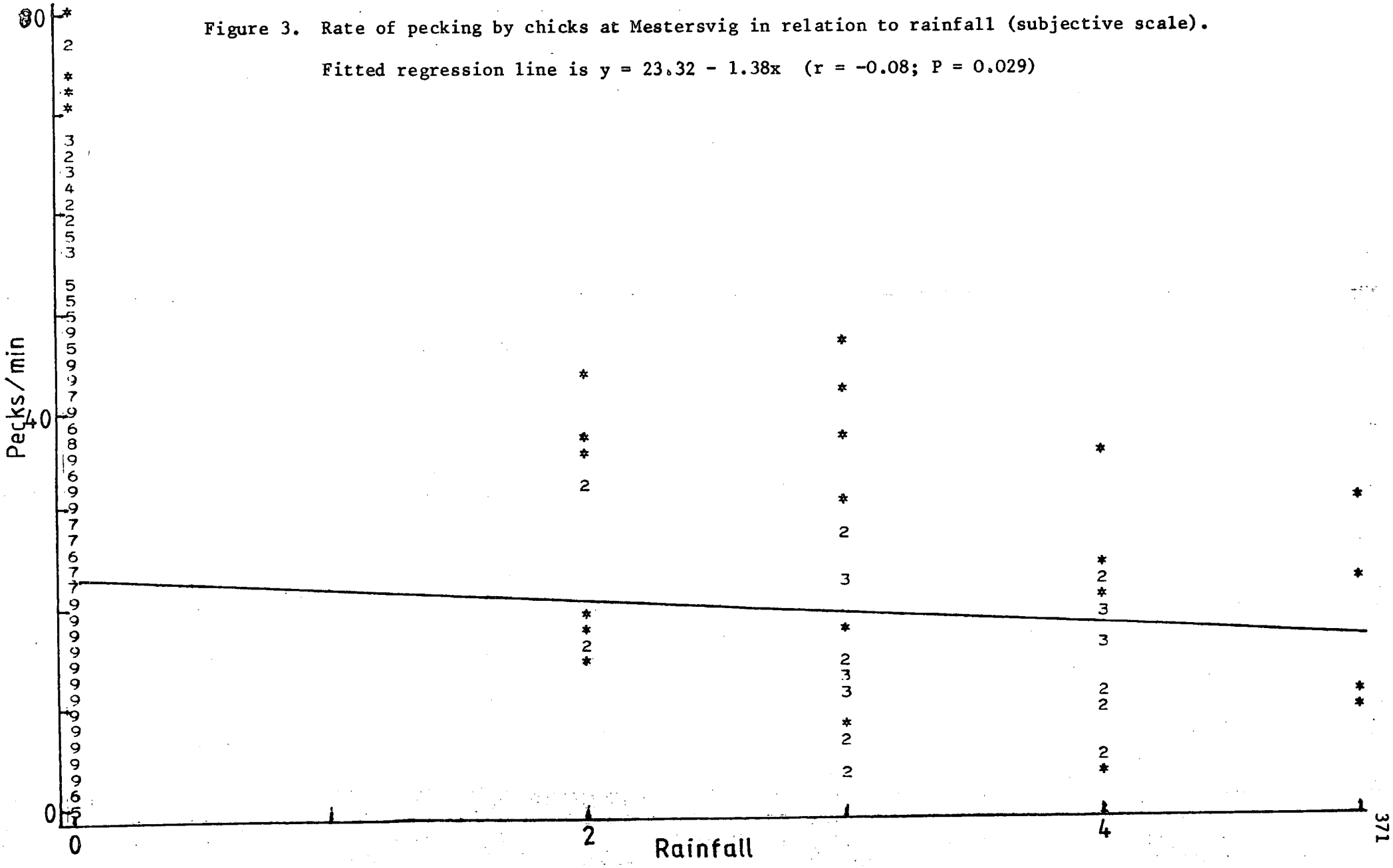


Figure 2. Rate of pecking by chicks at Mestersvig in relation to air temperature.

Fitted regression line is $y = 1.95x + 8.12$
($r = 0.36$; $P < 0.00001$)

Figure 3. Rate of pecking by chicks at Mestersvig in relation to rainfall (subjective scale).

Fitted regression line is y = 23.32 - 1.38x (r = -0.08; P = 0.029)



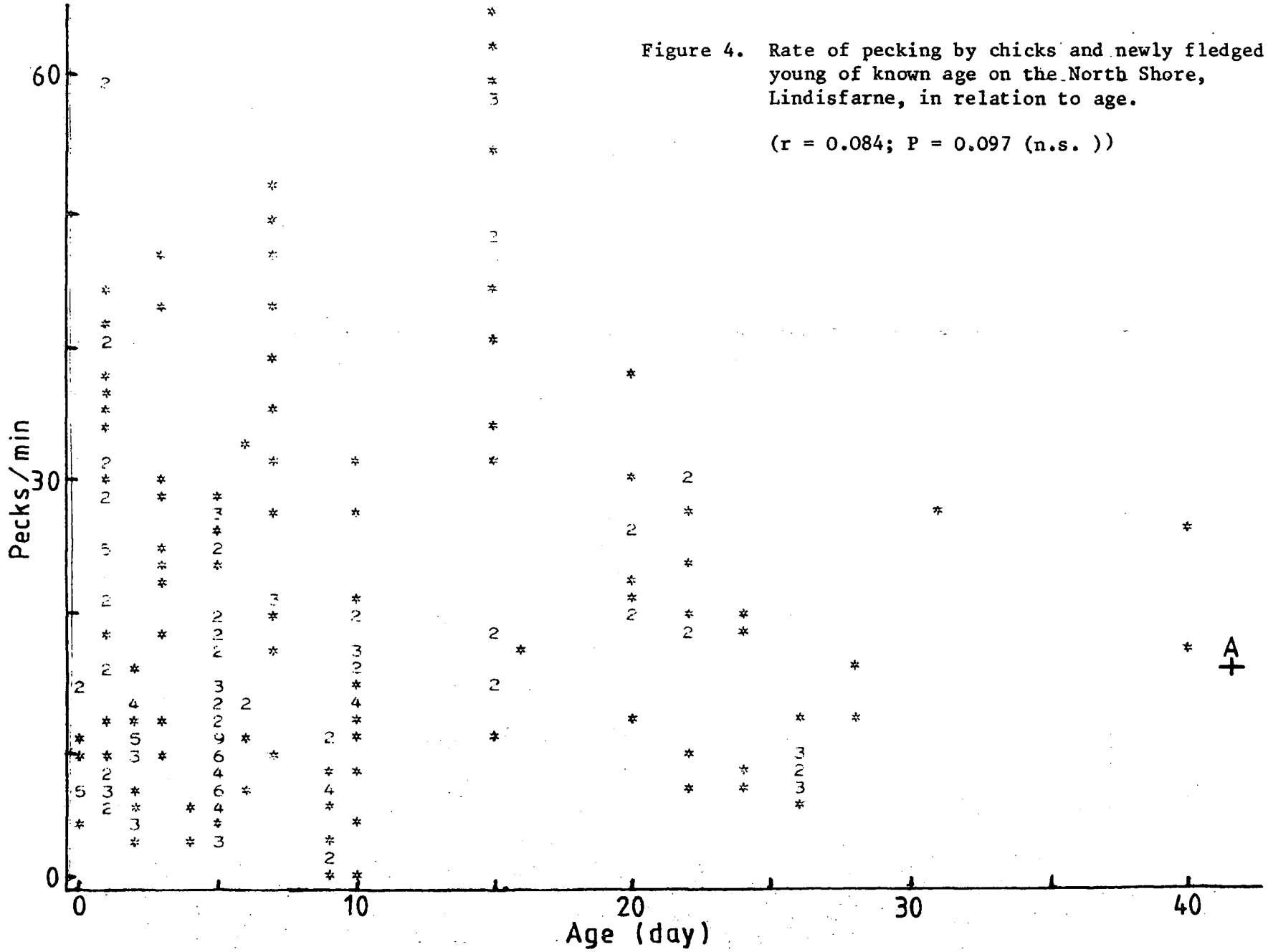


Figure 4. Rate of pecking by chicks and newly fledged young of known age on the North Shore, Lindisfarne, in relation to age.

(r = 0.084; P = 0.097 (n.s.))

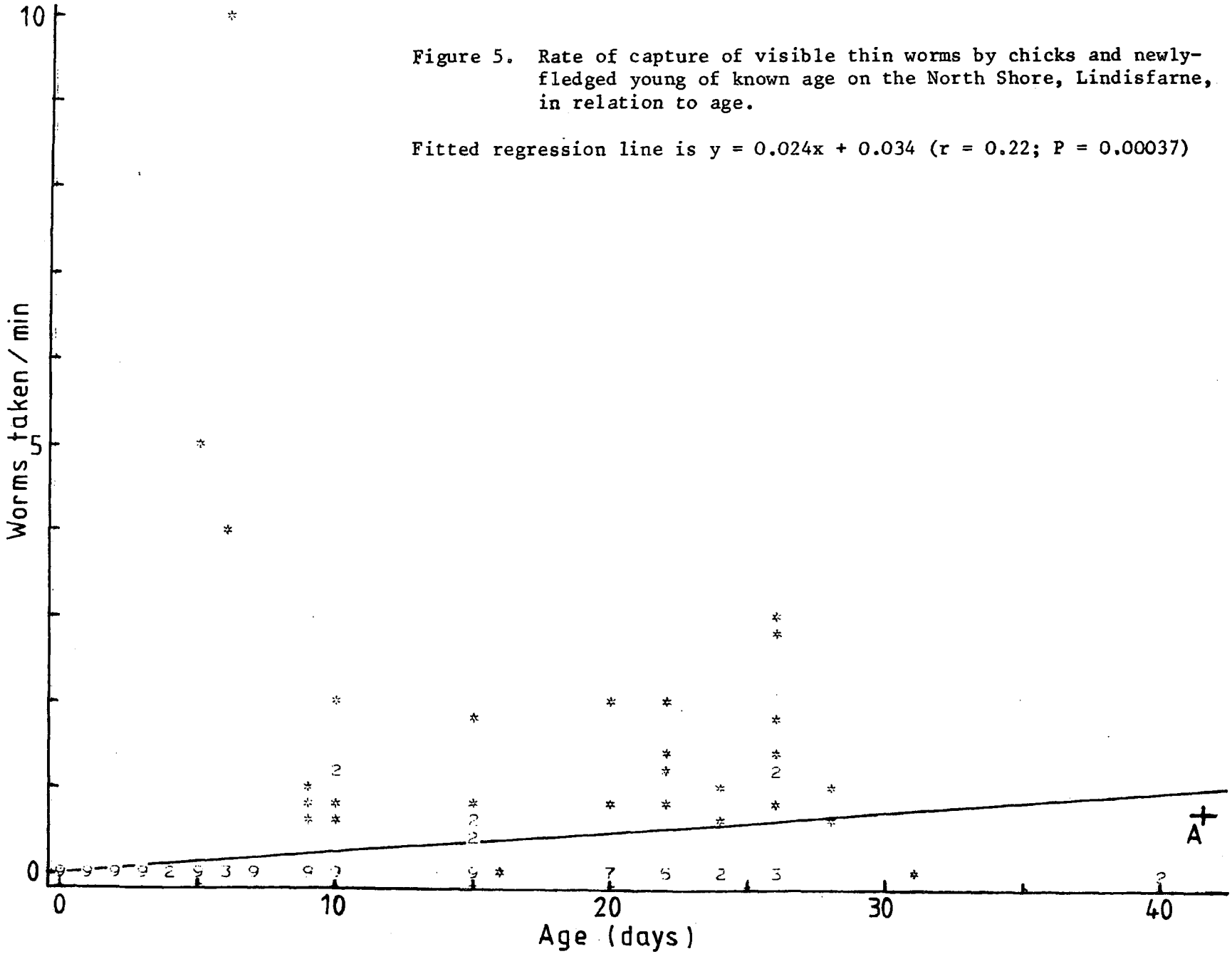


Figure 5. Rate of capture of visible thin worms by chicks and newly-fledged young of known age on the North Shore, Lindisfarne, in relation to age.

Fitted regression line is y = 0.024x + 0.034 (r = 0.22; P = 0.00037)

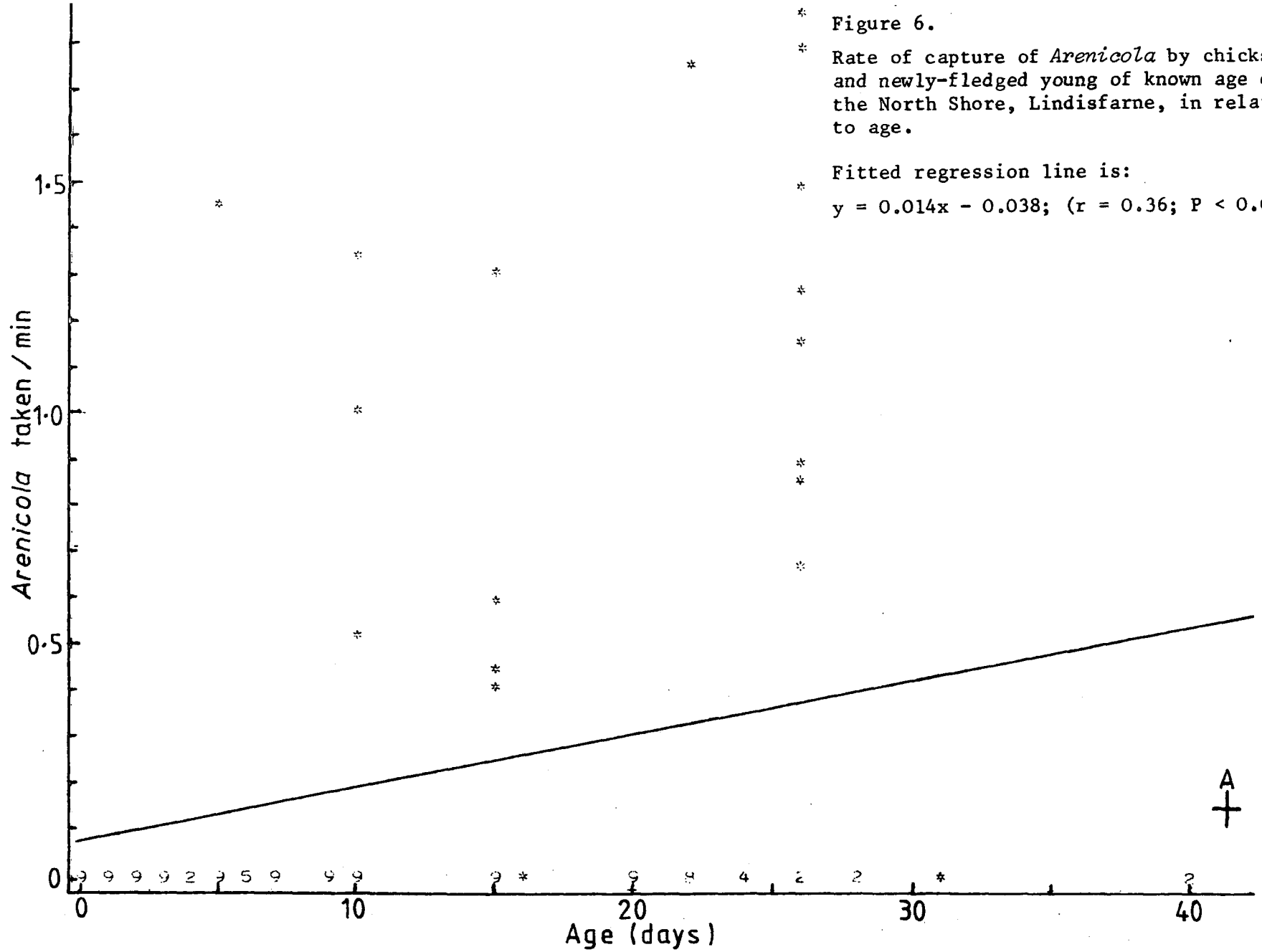


Figure 6.

Rate of capture of *Arenicola* by chicks and newly-fledged young of known age on the North Shore, Lindisfarne, in relation to age.

Fitted regression line is:

$y = 0.014x - 0.038$; ($r = 0.36$; $P < 0.00001$)

Figure 7. Rate of capture of observed prey by chicks and newly-fledged young of known age on the North Shore, Lindisfarne, in relation to age.

Fitted regression line is $y = 0.425x + 0.236$; ($r = 0.46$; $P < 0.00001$)

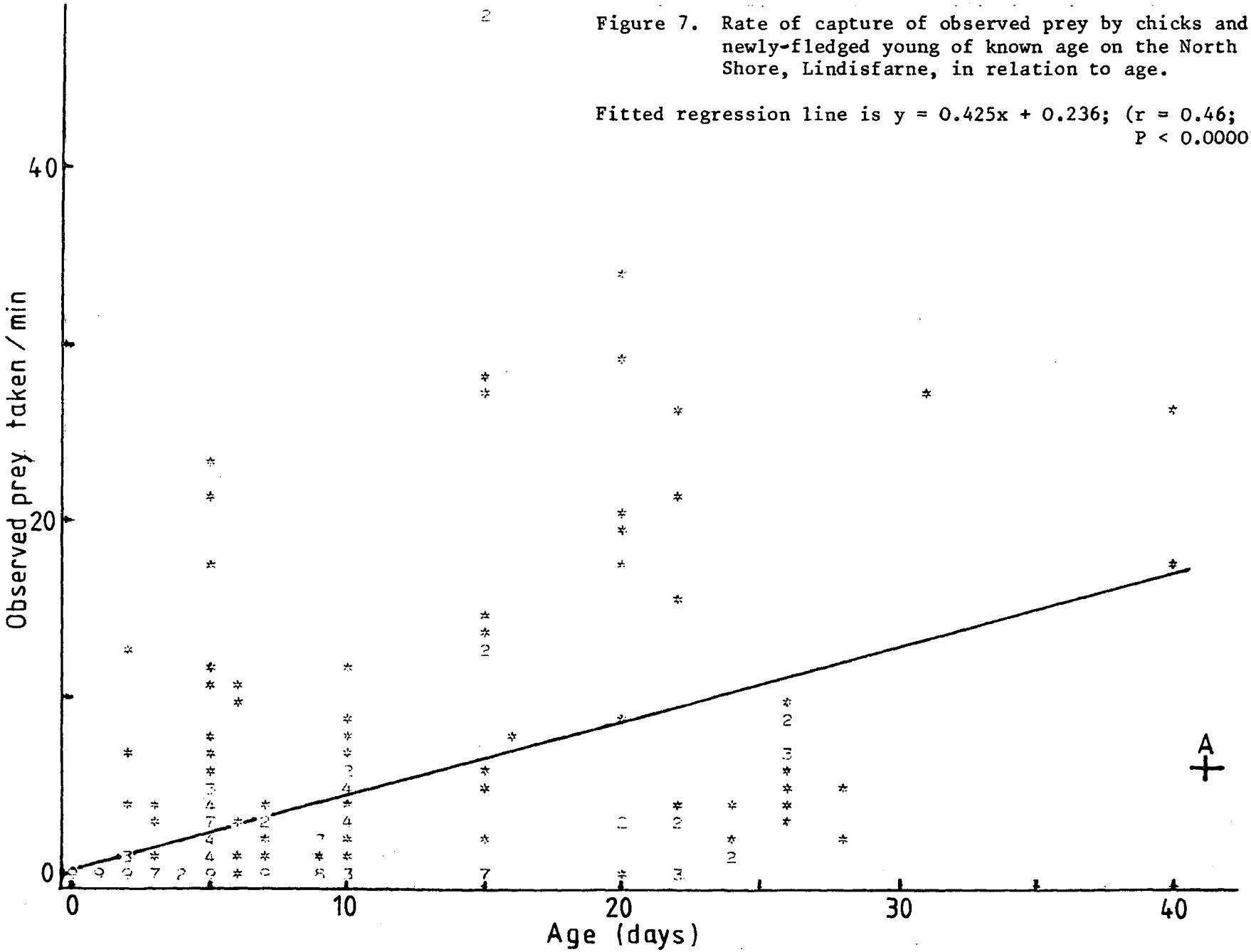
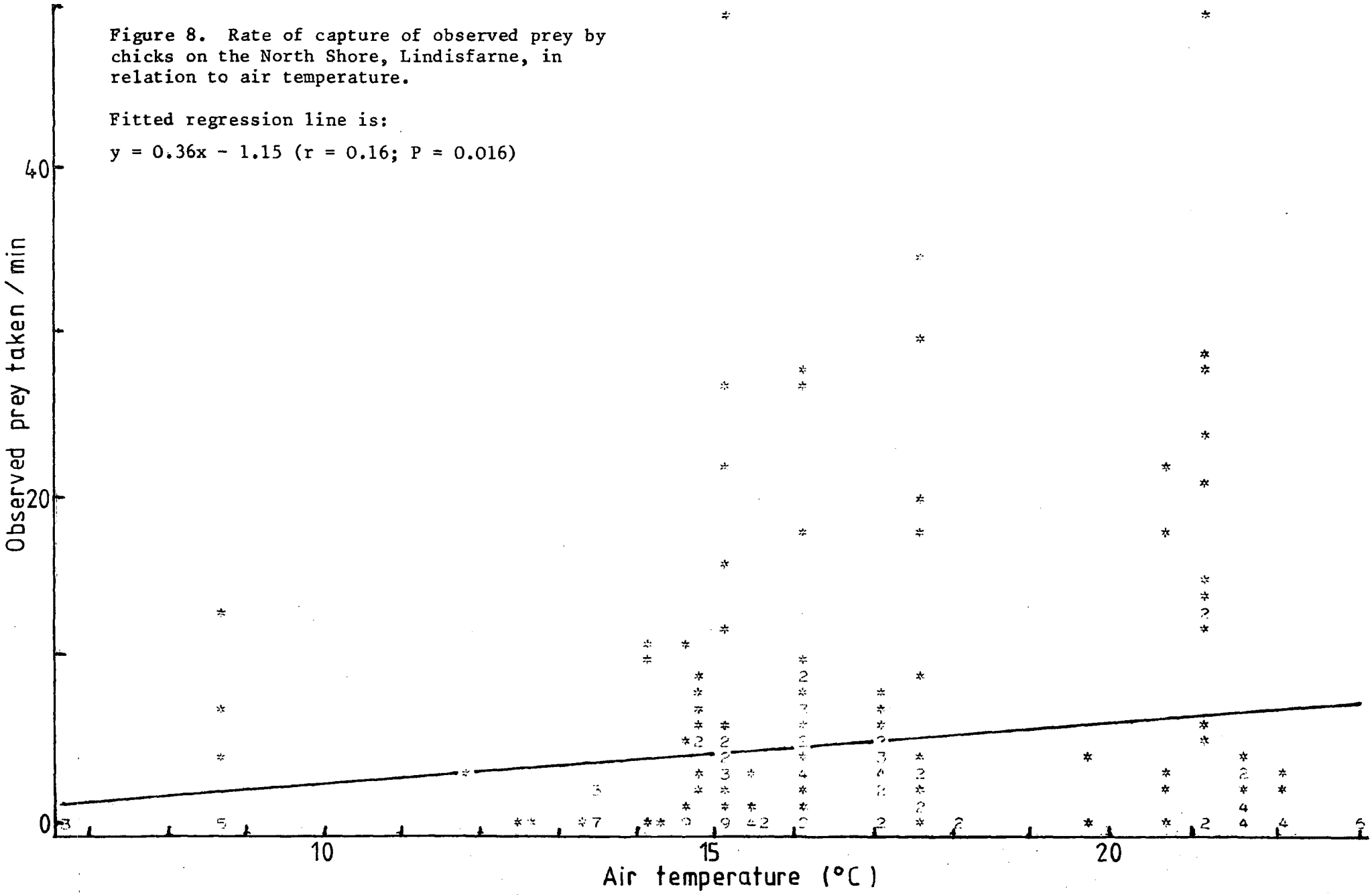


Figure 8. Rate of capture of observed prey by chicks on the North Shore, Lindisfarne, in relation to air temperature.

Fitted regression line is:

$y = 0.36x - 1.15$ ($r = 0.16$; $P = 0.016$)



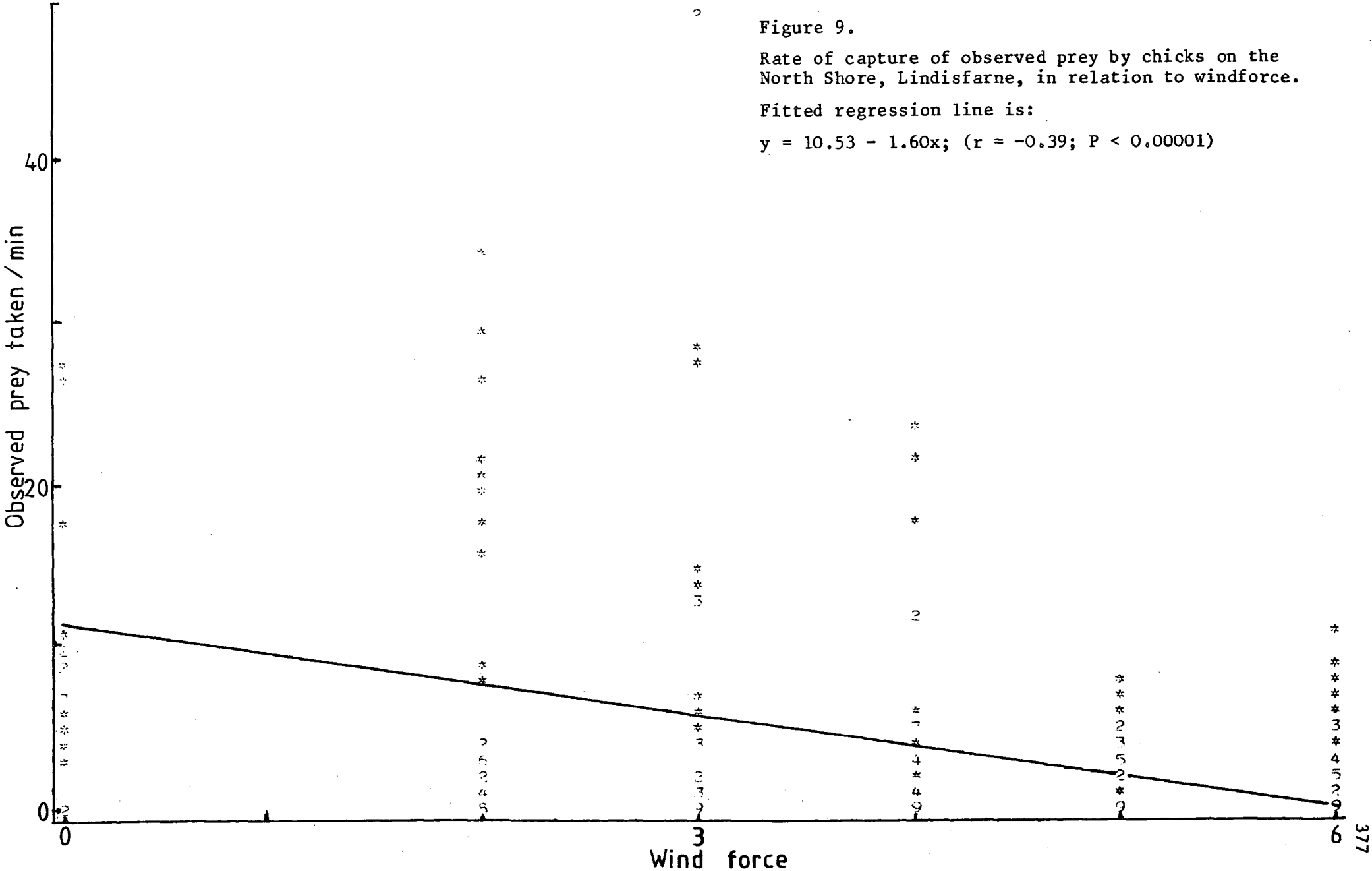


Figure 9.

Rate of capture of observed prey by chicks on the North Shore, Lindisfarne, in relation to windforce.

Fitted regression line is:

$y = 10.53 - 1.60x$; ($r = -0.39$; $P < 0.00001$)

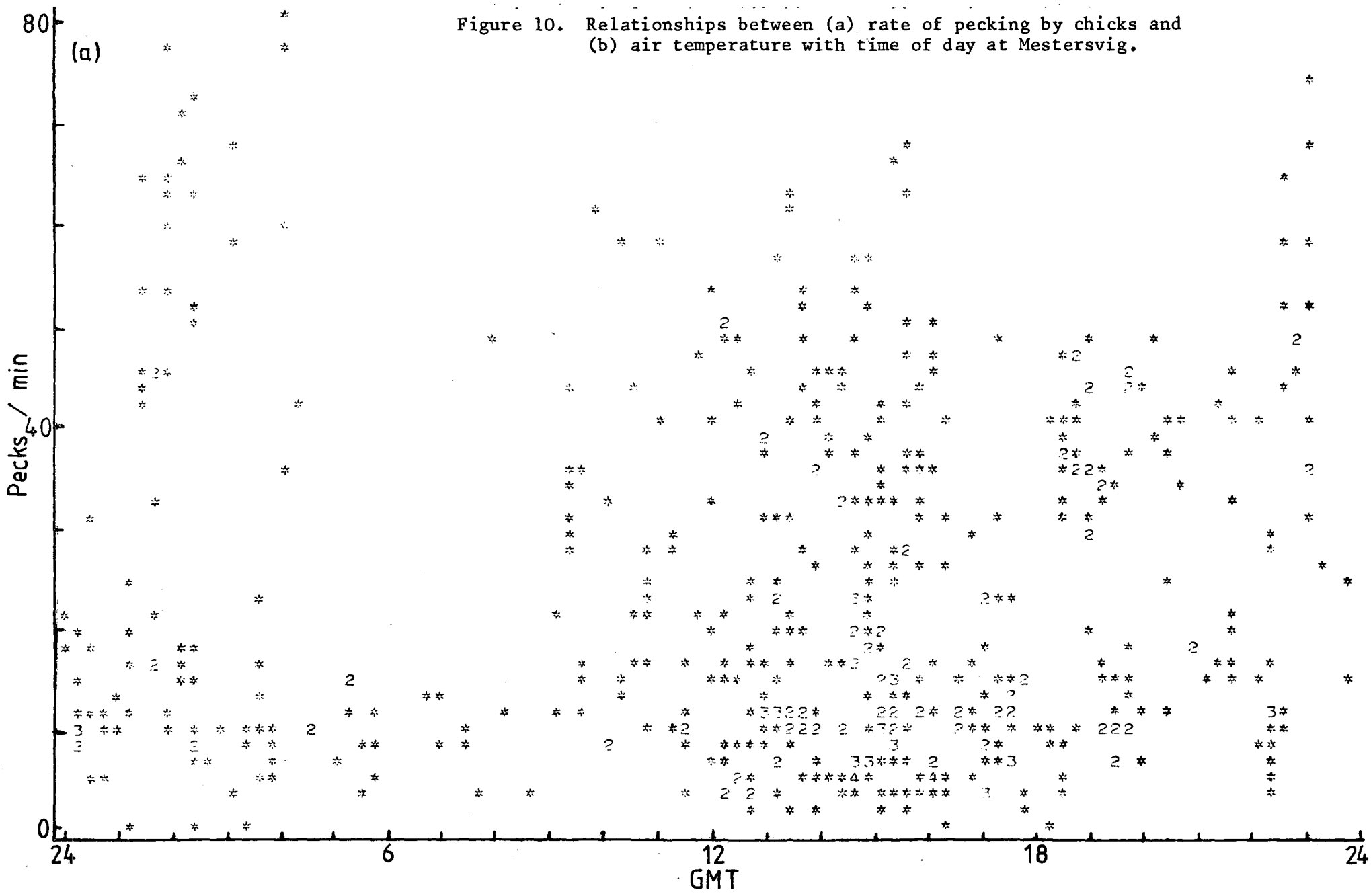
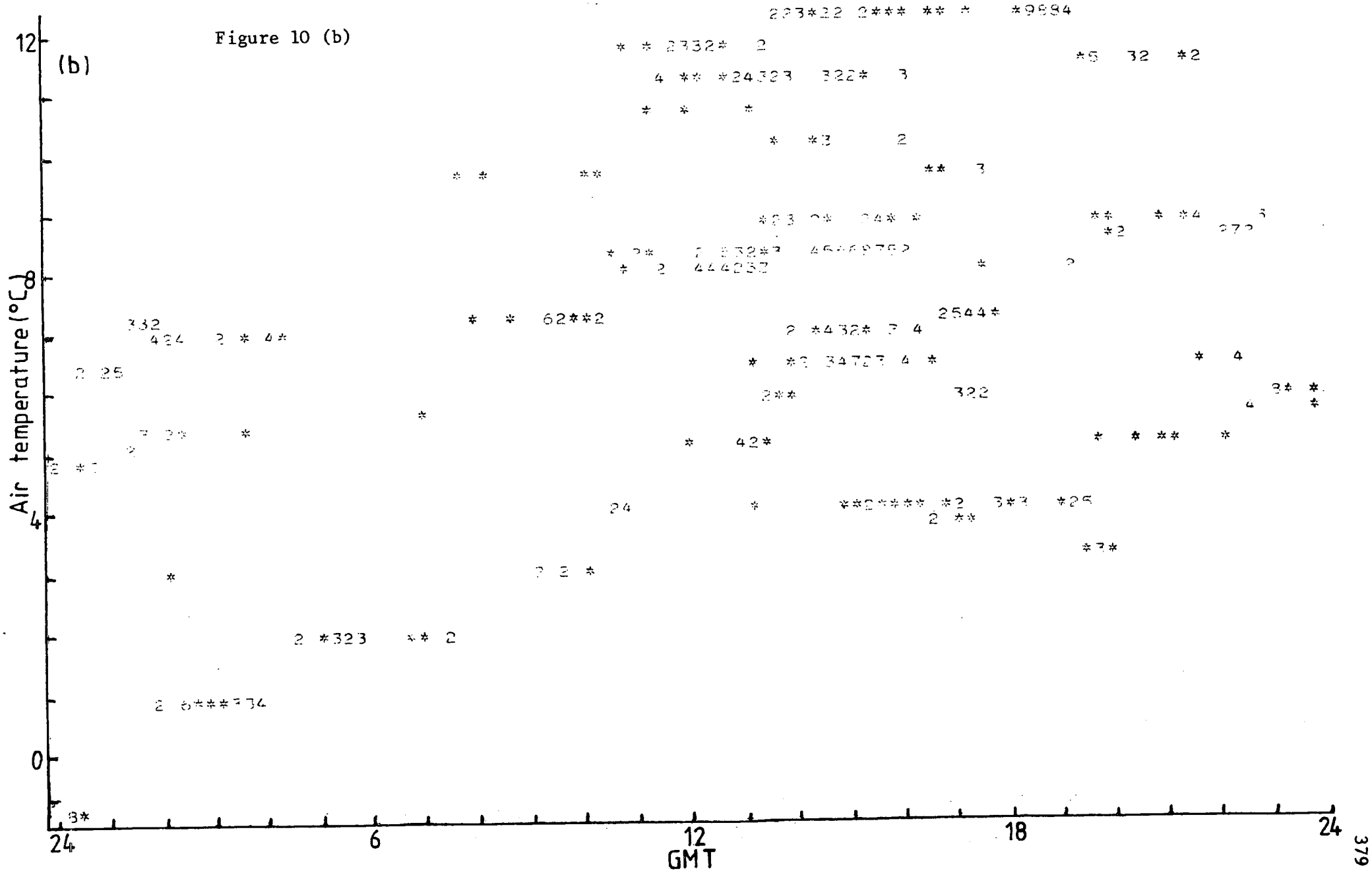


Figure 10. Relationships between (a) rate of pecking by chicks and (b) air temperature with time of day at Mestersvig.

Figure 10 (b)



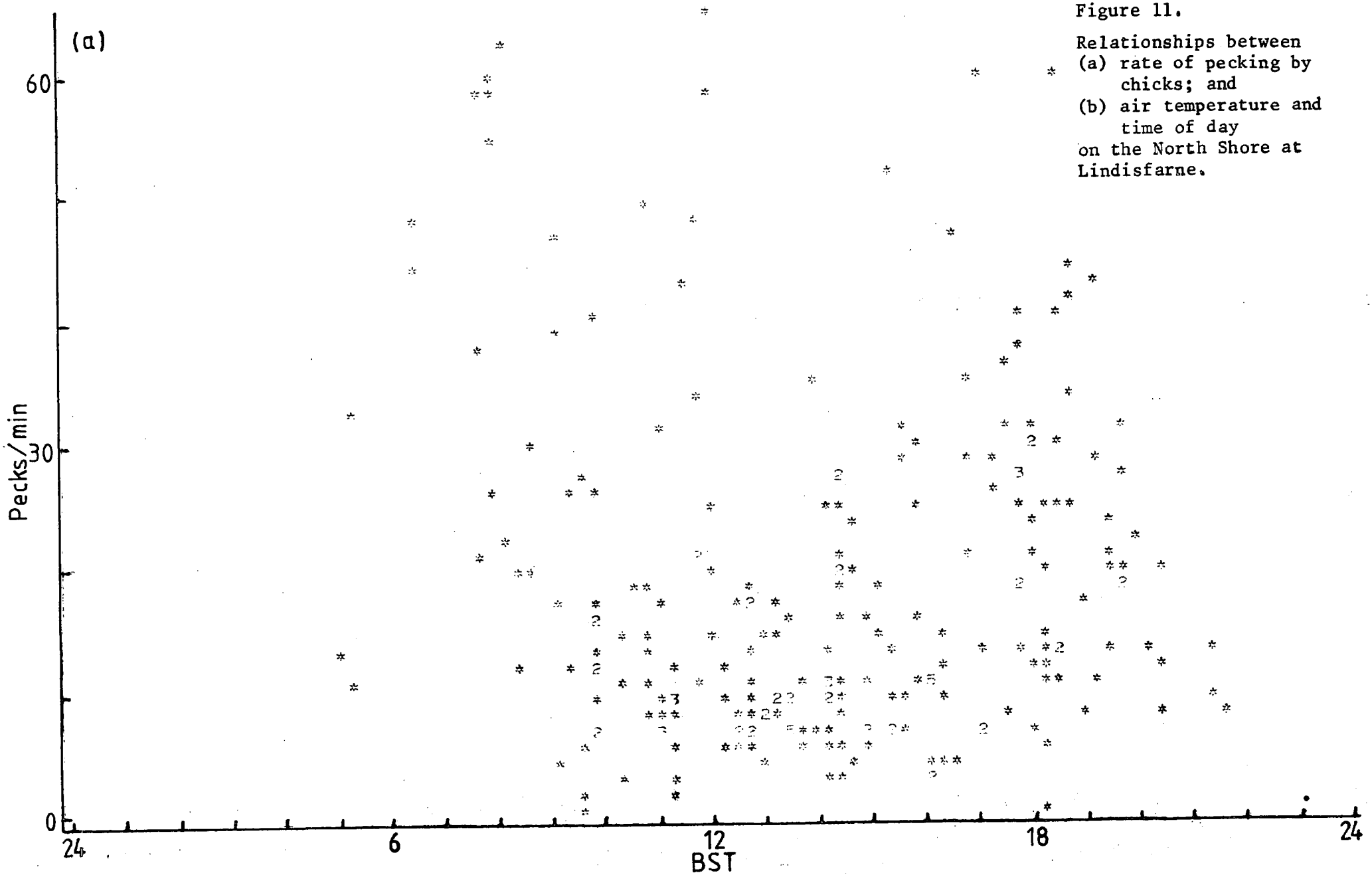


Figure 11.

Relationships between
(a) rate of pecking by chicks; and
(b) air temperature and time of day
on the North Shore at Lindisfarne.

Figure 11 (b)

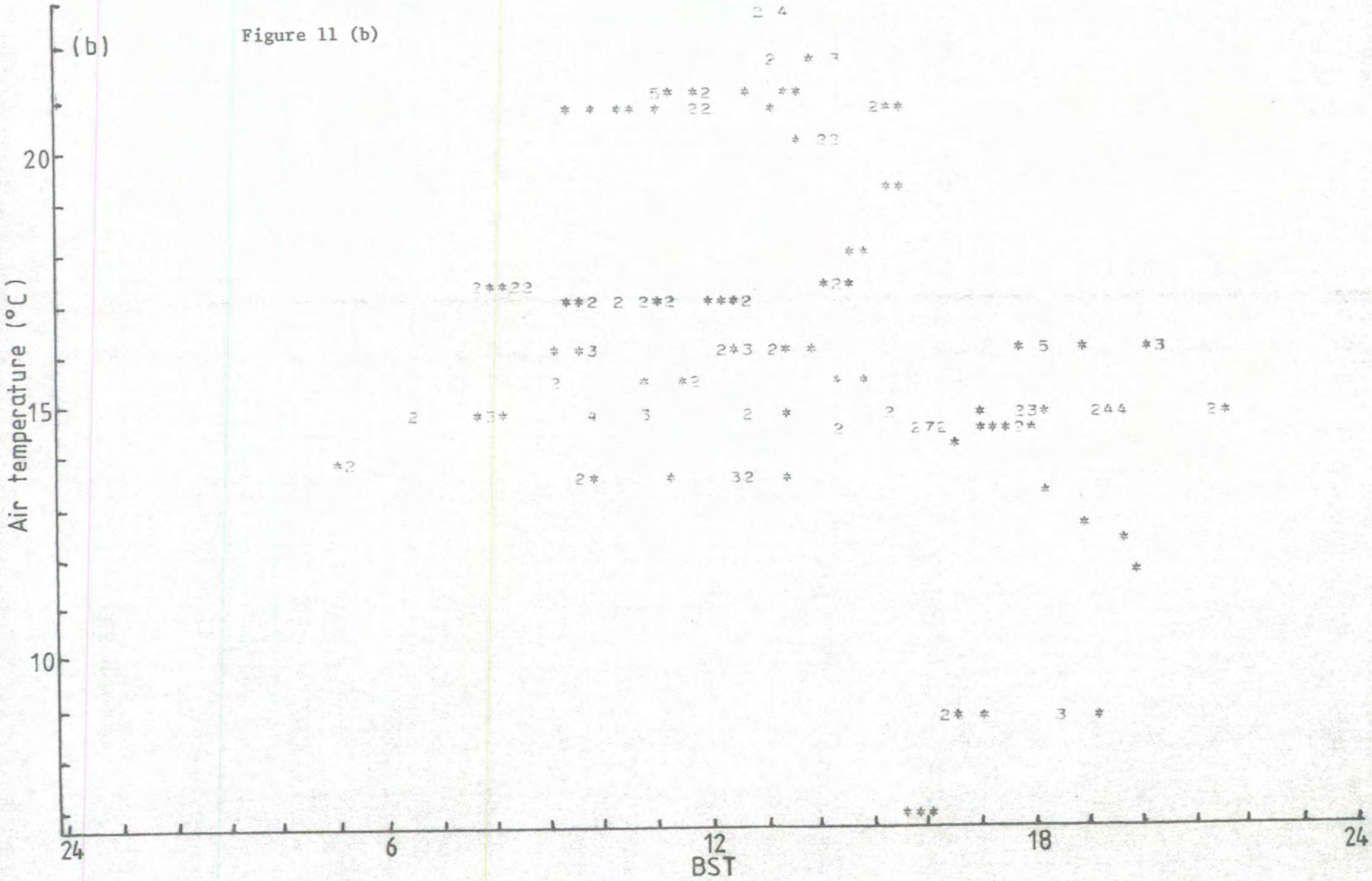
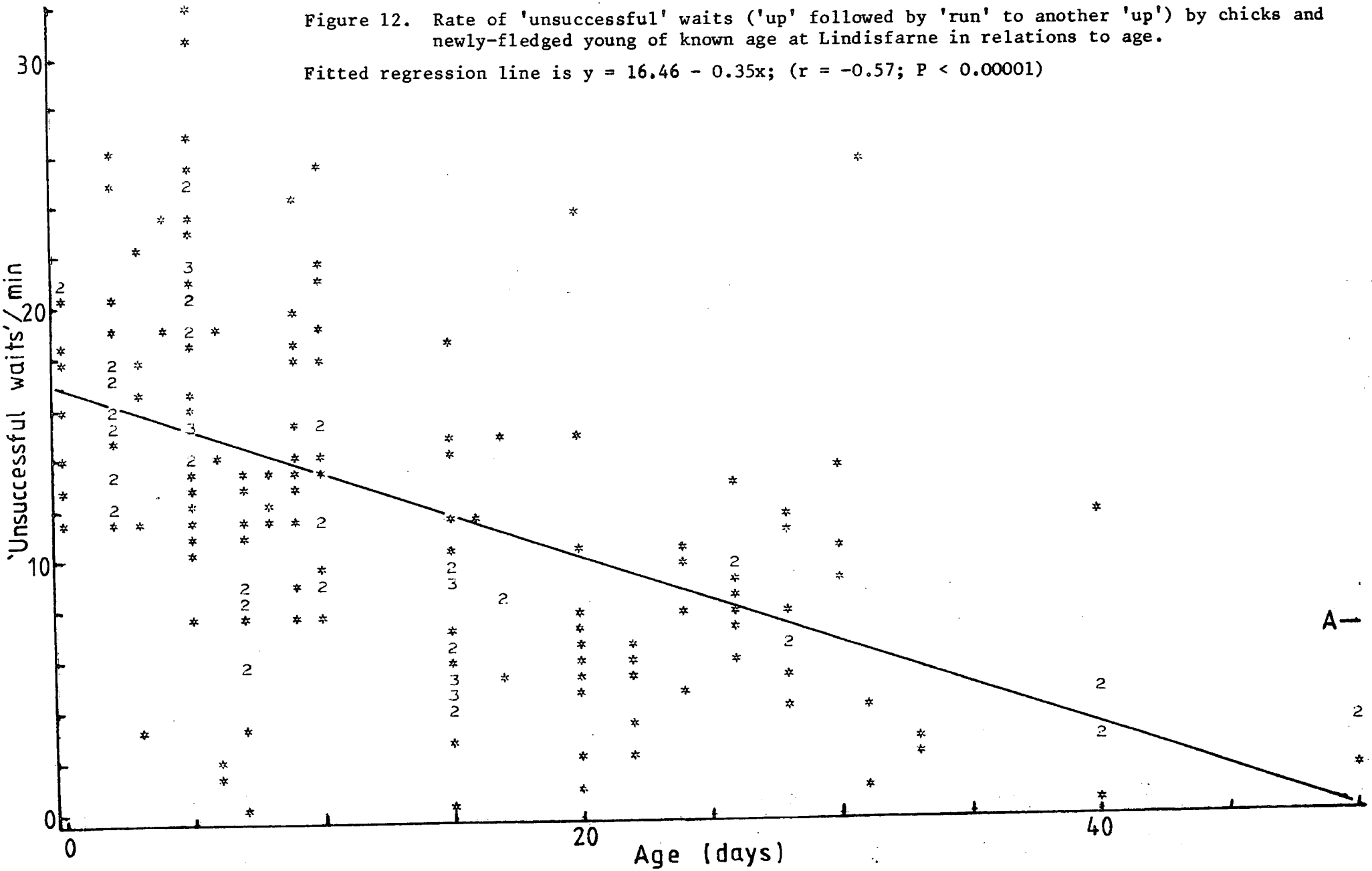


Figure 12. Rate of 'unsuccessful' waits ('up' followed by 'run' to another 'up') by chicks and newly-fledged young of known age at Lindisfarne in relations to age.

Fitted regression line is y = 16.46 - 0.35x; (r = -0.57; P < 0.00001)



Appendix 5. Prey abundance and availability in the breeding season of Ringed Plovers

Information on the intertidal invertebrates at Lindisfarne are detailed in Papers 1 & 2 and Appendices 1 & 2. Seasonal fluctuations in 'terrestrial' (i.e. not inter-tidal) prey abundance in the breeding season at both Mestersvig and Lindisfarne (see Papers 3 and 4) were monitored by pitfall traps. Each trap consisted of a white plastic carton 6.5 cm in diameter set in a hole with its opening flush with the ground. In Greenland each trap contained to a depth of a few centimetres a saturated solution of phenyl mercuric acetate, with a little liquid soap to reduce surface tension. At Lindisfarne, only water and liquid soap were used because of the public nature of the site. Traps were set in groups of 10 spaced at 1 m intervals along two lines of five, 1 m between lines. The traps were emptied weekly by pouring the contents through a sieve (mesh size approximately 0.4 x 0.8 mm) and transferringwith light forceps the contents to a storage vial for later sorting and counting. In Greenland, the contents of all ten traps at each site were collected together. At Lindisfarne, the contents from each trap were kept separate as traps there tended to suffer erratically from blowing sand and human interference, the latter resulting in the loss of all samples on a few occasions in July and August. Because of this the results are expressed as mean numbers per pitfall. In Greenland all the sampling was conducted in collaboration with the Dundee University team who were responsible for sorting and counting (see Greenwood 1978, who also discussed methodology and problems in more detail).

The results of invertebrate sampling at Mestersvig are detailed by Green, Greenwood & Lloyd (1977) and Greenwood (1978). To sample potential "terrestrial" prey on the North Shore at Lindisfarne, two sets of pitfall traps were used, one just above the high water mark of spring tides where most of the nests were found and one on a raised

gravel platform about 10 m behind. Although the birds (especially the young) did not feed much on the platforms (and prey were clearly less available there - Fig. 1) this set on the more stable substrate are of use as the pitfalls were less prone to sand filling than those on the shore. The accuracy of the results from the latter suffer from this, the high numbers of prey caught, and the high evaporation which combined to cause their efficiency of capture to vary considerably. This, together with weather effects on prey activity, is the probable reason for the tendency for some parallel variations in numbers of different animals trapped (Fig. 1) and the high variances (not shown). Indeed, it is probably unreasonable to consider the variations in numbers as matching any realistic pattern rather than indicating the presence of very large numbers of prey on the shore and fairly large on the gravel platform. Other points indicated are possibly increased tendencies for sandhoppers to occur on the platform early and late in the season; this may have been because high winds at these times moved sand onto this area. Also, the numbers of flies increased markedly in April and early May.

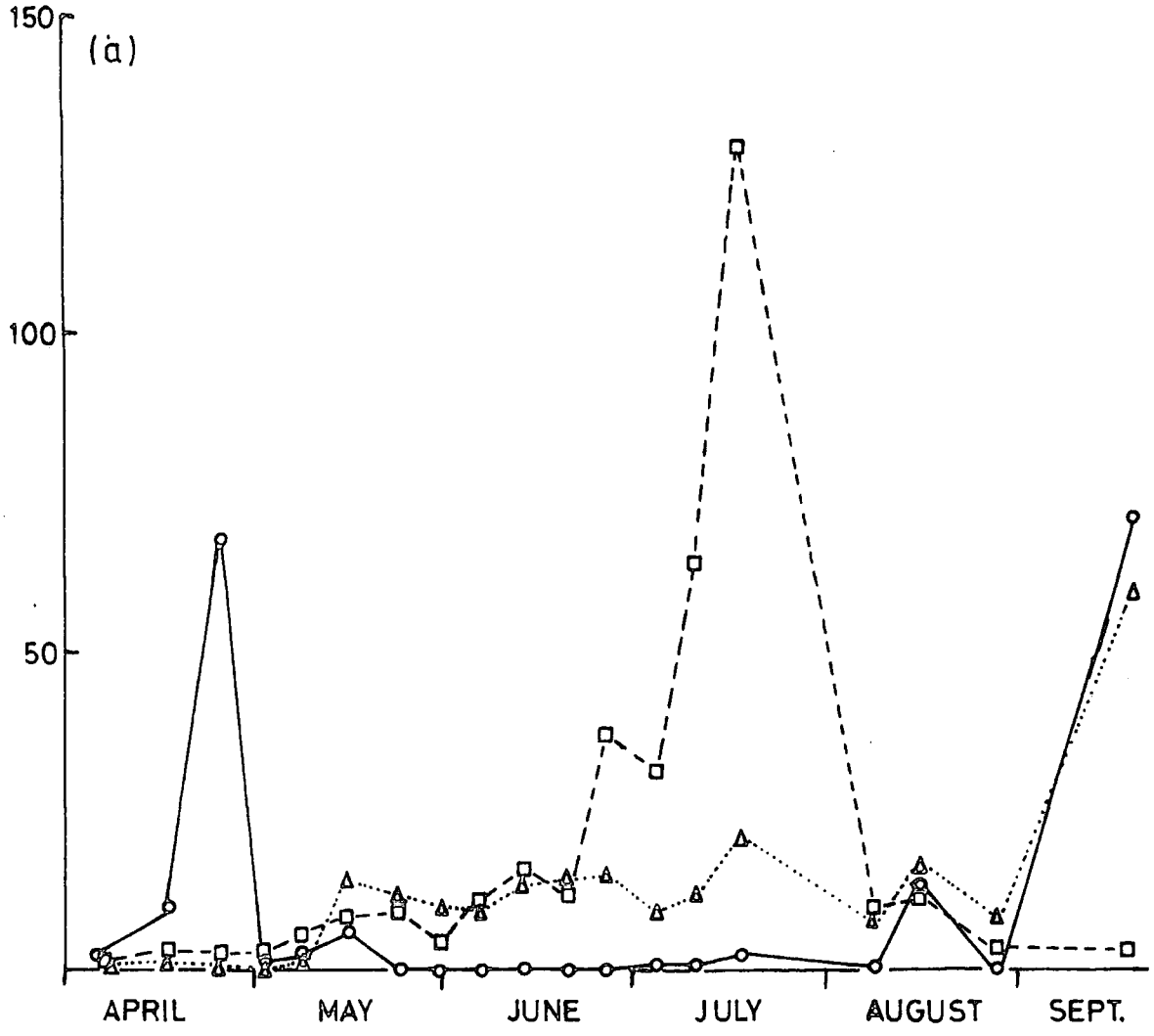


Figure 1. Mean numbers of main prey animals caught in pitfall traps on the North Shore at Lindisfarne in 1976.

(a) Gravel platform behind shore; (b) Shore

o—o sandhoppers

Δ·····Δ flies 5 - 10 mm length

□--□ flies 2 - 3 mm length

(Gap in data in July - August due to human interference)

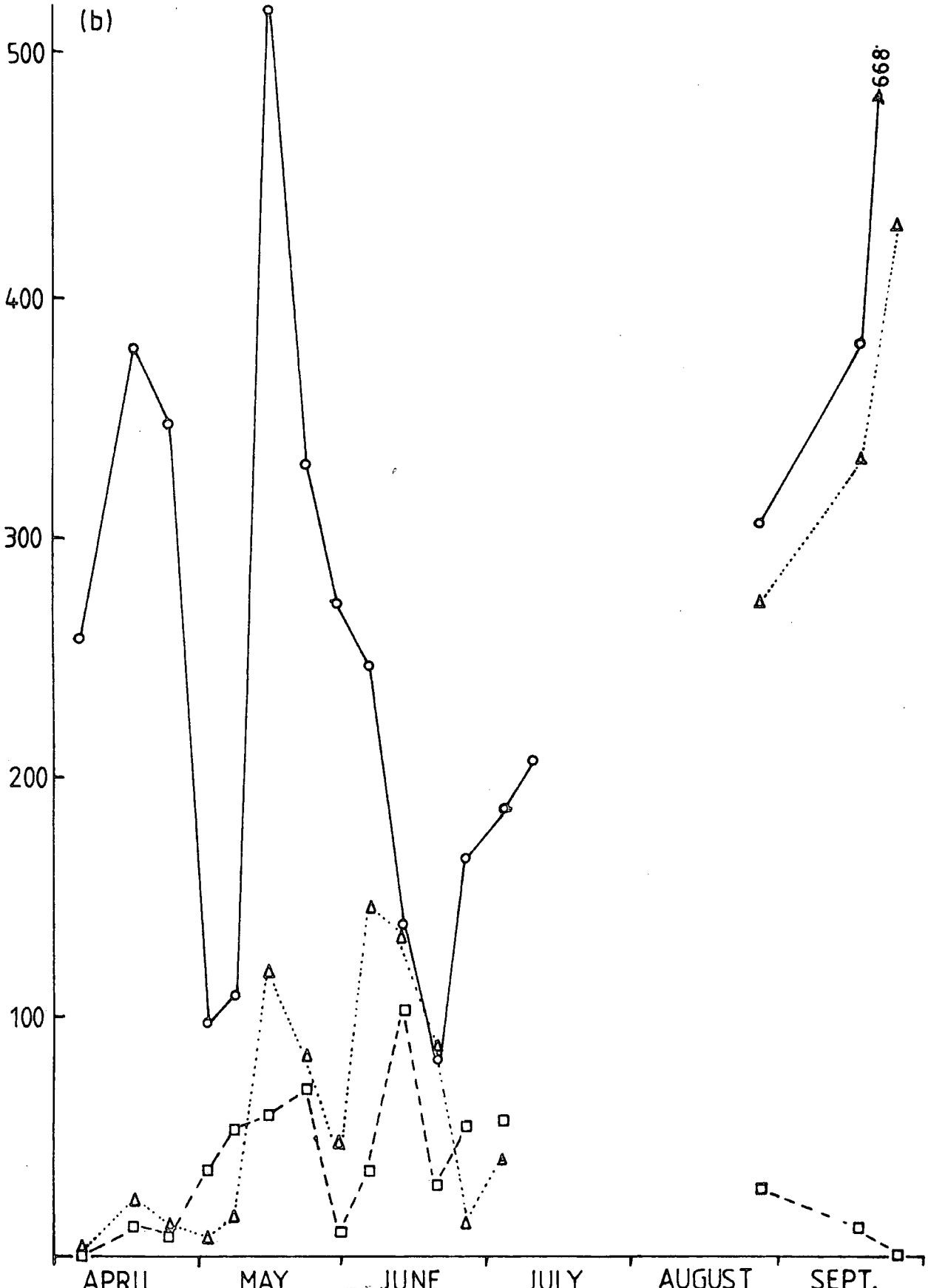


Figure 1(b)